GEORG-AUGUST-UNIVERSITÄT
GÖTTINGEN

The effects of ovulatory cycle shifts in steroid hormones on women's mate preferences and attraction

Dissertation
zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades
„*Doctor rerum naturalium*"
der Georg-August-Universität Göttingen

im Promotionsprogramm Behavior and Cognition
der Georg-August University School of Science (GAUSS)

vorgelegt von
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aus Gießen

Göttingen, 2018

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Danksagung

Ich danke den Menschen, die in den vergangenen Jahren direkt oder indirekt an meinem Dissertationsprojekt mitgewirkt haben. Sie haben mir durch Unterstützung und Freundschaft maßgeblich den Weg bereitet und ohne sie wäre mein Dissertationsprojekt möglicherweise nie zu Ende gekommen.

Mein aufrichtiger Dank gilt zunächst meinem Doktorvater, Lars Penke. Seine Anregungen, Ratschläge, Ideen, Expertise, Unterstützung, Wertschätzung, stets offene Tür und Begeisterung für die Wissenschaft haben mich sehr geprägt und maßgeblich zum Ablauf meiner Promotion beigetragen.

Meinen anderen beiden Thesis Committee Mitgliedern Mitja Back und Julia Ostner für Ratschläge und Unterstützung, die ebenfalls für den erfolgreichen Verlauf meiner Promotion mitverantwortlich sind.

Anne Schacht, Stefan Schulz-Hardt und Margarete Boos für die Bereitschaft meinem Promotionskommittee anzugehören und meiner Disputation beizuwohnen.

Meinen aktuellen und ehemaligen Kolleginnen und Kollegen (und gleichzeitig Freunden) Tanja, Ruben, Christoph, Tobi, Julie und Aileen, sowie Johanna, Christian und Adi für ihre Hilfe, Tipps, Unterstützung, Feedback, Ablenkung und offene Ohren. Ihr habt maßgeblich zu meiner Entwicklung und meinem Wohlbefinden in den letzten Jahren beigetragen.

My co-authors Natalie Motta-Mena, Rodrigo Cardenas, Drew Bailey, Kevin Rosenfield, Christoph Schild and David Puts, for sharing their data, valuable constructive feedback and support.

Jim, Dan, Katy, Rachel, Steve, Marco, Tran, Marley, Ben, Talia and the others with whom I had great times during my lab visits and at conferences. Thank you for having me, supporting my scientific career and being amazing science-friends.

Meinen Hilfskräften Laura, Laura, Paulina, Salome und Silvia. Ohne euch hätte ich die Daten für meine Dissertation nicht erheben können. Danke für euren Fleiß, euer Engagement und eure Zuverlässigkeit. Unsere freundschaftliche Zusammenarbeit lag mir immer besonders am Herzen und war sehr wichtig für den Verlauf meiner Promotion.

Ich danke meiner Familie und meinen Freunden, insbesondere meinem Bruder Jonas, Sophia, Filli, Nadine, Cora, Kaje, Simon, Katja, Svenja, Leonie, Lena, Vanessa, Freddy, Lena, Henrik, Fabi, Anna, Lisa, Janina, Nils, Markus und Felix. Ihr seid mir nach wie vor besonders wichtig. Danke für die gemeinsamen Wege durch Schule, Studium und Promotion, das Lecken von Wunden, fürs willkommene Ablenkungen sorgen und einfach fürs „immer für mich da sein".

Ein besonderer Dank gilt meinen Eltern, die mir mein Studium ermöglicht und mir stets liebevoll, bedingungslos und unterstützend zur Seite gestanden haben.

Abschließend möchte ich Alex danken. Für seine stetige Ermunterung, bedingungslose Unterstützung, Motivation und liebevolle Begleitung in allen Lebenslagen. Worte reichen nicht aus um meinen Dank dir gegenüber zu beschreiben.

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Appendix D. Curriculum Vitae

Preface

This dissertation is not a cumulative, publication-based dissertation, but follows it in form. It includes three manuscripts, one of which has been accepted for publication, two of which are preprints of manuscripts that are currently in preparation for resubmission or under review.

Jünger, J., Kordsmeyer, T. L., Gerlach, T. M., & Penke, L. (2018). Fertile women evaluate male bodies as more attractive, regardless of masculinity. *Evolution and Human Behavior*, *39*, 412-423. DOI: 10.1016/j.evolhumbehav.2018.03.007

Jünger, J., Gerlach, T. M., & Penke, L. (2018). *No evidence for ovulatory cycle shifts in women's preferences for men's behaviors in a pre-registered study*. Manuscript in preparation for resubmission. Preprint retrieved from psyarxiv.com/7g3xc. DOI: 10.17605/OSF.IO/7G3XC

Jünger, J., Motta-Mena, N. V., Cardenas, R., Bailey, D., Rosenfield, K. A., Schild, C., Penke, L., & Puts, D. A. (2018). *Do women's preferences for masculine voices shift across the ovulatory cycle*? Manuscript submitted for publication. Preprint retrieved from psyarxiv.com/k9y7s DOI: 10.17605/OSF.IO/K9Y7S

1. Introduction

Do women's mate preferences and attraction change across the ovulatory cycle? This is a central question in human evolutionary sciences. Psychological changes, especially shifting mate preferences, across the ovulatory cycle have long been seen as evidence that women's mating psychology has been shaped by sexual selection (e.g. Buss & Schmitt, 2011). A large amount of studies have sought to investigate how women's sexual interests, desire, mate preferences and behavior systematically change across the cycle, regulated by changes in steroid hormone levels. However, during the last years, there have been several large-scale failures to replicate effects that were formerly thought to be well-established. Hence, there is no clear consensual agreement about the existence of psychological and behavioral changes across women's ovulatory cycle.

This dissertation focuses on possible shifts in women's mate attraction and preferences across the ovulatory cycle, that might be connected to changes in sexual desire and interest. The mediating role of steroid hormones and possible moderating variables, such as women's relationship status and self-reported stress, will be addressed. To contribute to the actual scientific discourse in ovulatory cycle research, we conducted a large within-subject study to investigate three possible dimensions for which cycle shifts have previously been reported: masculine bodies, behaviors and voices. Findings are reported in three separate manuscripts. Although they can not conclusively answer if any mate preference changes across the cycle exist, they lead to important implications and directions for future research.

1.1 Do human females show estrus?

The concept of estrus stems from mammalian reproductive biology and is defined as a "relatively brief period of proceptivity, receptivity, and attractivity in female mammals that usually, but not invariably, coincides with their brief period of fertility" (Symons, 1979, p.97). It describes the circumstance that females of non-human mammals typically engage in sex in their fertile phase when conception is possible, but not in other, non-fertile phases of their estrous cycle. The different states of estrus are thought to be generated by reproductive hormones, especially estrogens (Gangestad, Thornhill, & Garver-Apgar, 2015). Although women experience ovarian hormonal changes across the ovulatory cycle that are somehow equivalent to the estrus cycle of non-human mammals, they appear equally sexually receptive throughout the whole cycle (Thornhill & Gangestad, 2015). This circumstance of non-conceptive sexuality is referred to as *extended sexuality* (Rodriguez-Girones & Enquist, 2001).

The fact that women experience extended sexuality led to the assumption that (classically defined) estrus was lost in human females, possibly to the emergence of male long-term investment in mates and offspring (Alexander & Noonan, 1979; Lovejoy, 2009; Strassmann, 1981; Symons, 1979). The reason behind this idea is that the concealment of women's ovulation would prevent men to compete to inseminate women only within their fertile phase and then move to other women as soon as they become fertile, without providing paternal investment in their offspring[1]. However, the lost estrus claim has been challenged by findings suggesting that there are, indeed, psychological and behavioral changes across the ovulatory cycle. Although these changes seem not to be as obvious as estrus changes in some non-human mammals, they suggest that estrus was not "lost" in humans, despite the evolution

[1] Based on the assumption that higher mating effort would reduce paternal effort and that higher paternal care could be a determinant for offspring success (e.g. Strassmann, 1981). However, there are several explanations for the evolution of long-term mating. Though, as it is not the focus of this dissertation, it will not be further discussed. See Buss and Schmitt (1993) or Conroy-Beam, Goetz and Buss (2015) for a detailed overview.

of extended sexuality (Thornhill & Gangestad, 2008). Nevertheless, women do not show "classic estrus" in a sense that they are only sexually active during a restricted fertile period. Rather, the nature of women's sexual interests change across the ovulatory cycle (Gangestad, 2017).

1.2 Dual sexuality and "good genes" sexual selection

To capture the idea that women's conceptive vs. non-conceptive sexual interests may not be identical, Thornhill and Gangestad (2008) proposed the concept of *dual sexuality*. While sexual behavior outside the fertile phase may have evolved for pair-bonding purposes, the most direct benefit for sexual behavior within the fertile phase is conception. Hence, sexual interests should vary across the cycle and reflect these benefits. More precisely, when women can conceive (in the fertile phase of their cycle) their sexual receptivity and proceptivity should be directed preferentially towards men who offer benefits that promote their offspring's fitness, therefore, features that are assumed to be associated with genetic benefits (Gangestad et al., 2015). Contrary, in their non-fertile phases, they should have more sexual interests related to pair-bond maintenance (Thornhill & Gangestad, 2008).

But what exactly does "good genes" mean? Good genes are defined as indicators of genetic fitness, including dyadic genetic fit (e.g. good immunocompetence genes), adaption to the current environment (e.g. having high fat reserves in a society that frequently faces starvation) and comparatively few harmful mutations (Arslan, 2017). There are some indicators of genetic quality in men, like symmetry or masculine traits that are particularly assumed to reflect men's genetic quality. These characteristics include facial or body masculinity, lower voice pitch, behavioral displays of dominance, and physical attractiveness (for reviews see Gangestad & Thornhill, 2008; Roney, 2009; Thornhill & Gangestad, 2008). Moreover, higher circulating testosterone levels are discussed to be an indicator of superior immune functioning (in line with the immunocompetence handicap hypothesis; Hamilton & Zuk, 1982). These masculine characteristics are seen as costly to produce and maintain (Gildersleeve, Haselton, & Fales, 2014a), hence, they are argued to reflect good genes because only highly fit individuals in good condition can afford to invest resources in these traits. Importantly, the concept of good genes has no direct correspondence in the evolutionary genetic literature (Arslan & Penke, 2015) and some purported indicators of good genes are controversial, because reported findings challenge the hypothesis that they actually signal heritable fitness benefits and immunocompetence (Scott, Clark, Boothroyd, & Penton-Voak, 2012; Scott et al., 2014; Simmons, Peters, & Rhodes, 2011; Wood, Kressel, Joshi, & Louie, 2014).

Although the concept of "good genes" is controversial, there is evidence that, in line with the dual sexuality assumption, women's sexual desire varies across the cycle. Women experience higher in-pair sexual desire during the non-fertile luteal phase (Grebe, Emery Thompson, & Gangestad, 2016), whereas extra-pair desire is reported to be higher in the fertile phase (Gangestad, Thornhill, & Garver, 2002; Gangestad, Thornhill, & Garver-Apgar, 2005b; Shimoda, Campbell, & Barton, 2018). Interestingly, women whose partners possess a lower genetic quality were proposed to be especially attracted to extra-pair mates when fertile (Gangestad et al., 2005b; but see Arslan, Schilling, Gerlach, & Penke, 2018; Shimoda et al., 2018). However, these findings were challenged by a recent higher powered, pre-registered study, reporting that both, in-pair and extra-pair sexual desire increase in the fertile phase and are lower in the luteal phase (Arslan et al., 2018). Importantly, in this study, partner's sexual attractiveness did not moderate changes in sexual desire (Arslan et al., 2018). Another study including direct assessment of ovarian hormones, reported fertile phase increases in in-pair and extra-pair desire, that were correlated with steroid hormone levels (Roney & Simmons, 2016). Moreover, further work showed evidence that general sexual desire (Jones et al., 2018b; Roney & Simmons, 2013), but not desire for uncommitted sexual relationships, tracks changes in women's hormonal status across the ovulatory cycle (Jones et al., 2018b). Hence, sexual interest in form of desire seems to vary across the cycle, but the reported studies did not directly investigate if these shifts in sexual desire are also reflected in varying mate attraction or preferences across the cycle. As implied above, Gangestad and Thornhill (1998; see also Thornhill & Gangestad, 2008) claimed that varying sexual interests across the cycle should have consequences for sire choice, with fertile phase sexual interests functioning to obtain good genes. Based on the same assumptions, Gangestad, Thornhill and Garver-Apgar (2005a) postulated the *ovulatory shift hypothesis* to directly describe how exactly women's mate preferences and choices should vary across the cycle.

1.3 The ovulatory shift hypothesis

The ovulatory shift hypothesis makes three directly testable predictions about shifts in women's mate preferences across the cycle (Gangestad et al., 2005a; Gildersleeve et al., 2014a): First, when fertile, women should be more sexually attracted to men's characteristics that reflect good genes, compared to their low-fertility days. Second, cycle shifts in women's mate preferences for good genes characteristics should be absent or only weakly present when evaluating men for long-term relationships. Third, when fertile, women should not be sexually attracted to men's characteristics that reflect a higher suitability as a long-term partner, compared to their low-fertility days. Pillsworth and Haselton (2006) even expanded these ideas and stated that women may have evolved a dual-mating strategy in which they secure investment through their (long-term) partner, while obtaining good genes for their offspring through extra-pair copulations with other men when fertile, especially when their partner lacks in displaying indicators of good genes. Since preferences for purported indicators of good genes are predicted to shift across the ovulatory cycle, potentially to obtain good genes through extra-pair copulations (Pillsworth & Haselton, 2006), I will further call this theory the *good genes ovulatory shift hypothesis* (henceforth GGOSH; see also Arslan et al., 2018).

1.3.1 Cycle shifts in mate preferences

Previous research has documented cycle shifts in women's mate preferences for several physical and behavioral traits. More precisely, it has been reported that, in their fertile phase, women indeed shift their preferences toward men possessing putative indicators of genetic quality, including masculine, dominant-appearing faces (e.g. Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), voices (Feinberg et al., 2006; Pisanski et al., 2014; Puts, 2005; 2006), bodies (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Little, Jones, & Burriss, 2007; Pawlowski & Jasienka, 2005), odor (Gangestad & Thornhill, 1998; Havliček, Roberts, & Flegr, 2005; Thornhill, Chapman, & Gangestad, 2013) and behavioral displays (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Gangestad et al., 2007). Instead of estimated cycle phase or conception risk, a number of studies rather worked with measured ovarian hormone levels to predict women's mate preferences and shifts, arguing that the ovulatory cycle is regulated by ovarian hormones, especially estradiol and progesterone. Whereas the fertile phase (late follicular phase) of the cycle is characterized by higher levels of estradiol and lower levels of progesterone, levels of estradiol are lower and levels of progesterone are higher during the luteal phase, when conception risk is low, except of a second smaller estradiol peak mid-luteal (Gangestad & Haselton, 2015; Puts et al., 2013). Hence, if preference shifts are indeed regulated by changes in steroid hormones, they should be regulated by changes in estradiol and progesterone (or their ratio). Indeed, in studies with direct hormone assessments, shifts in women's mate preferences were predicted by changes in estradiol and progesterone levels (Ditzen, Palm-Fischbacher, Gossweiler, Stucky, & Ehlert, 2017; Feinberg et al., 2006; Pisanski et al., 2014; Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011). Comparable results were found in studies with estimated hormone levels (Lukaszewski & Roney, 2009; Puts, 2006). Additionally, other research also indicated that changes in testosterone (Bobst, Sauter, Foppa, & Lobmaier, 2014; Welling et al., 2007) or cortisol (Ditzen et al., 2017) might also influence women's mate preferences. Testosterone also varies slightly, but systematically across the cycle (Puts, 2006; Roney & Simmons, 2013). Furthermore, cortisol was found to be induced by stress (Herrera, Nielsen, & Mather, 2016), sometimes inhibiting estradiol emission in young women (Roney & Simmons, 2015).

1.3.2 Contradictory evidence not supporting the GGOSH

Although the above mentioned findings create the impression that evidence for cycle shifts in women's mate preferences is robust, evidence for the GGOSH is, in fact, inconclusive. In 2014, after most of the mentioned studies were already published, two meta-analyses came to opposing conclusions regarding the existence of cycle shifts (Gildersleeve et al., 2014a; Wood, et al., 2014). Wood and colleagues (2014) evaluated 58 independent reports (45 published, 13 unpublished), and concluded that the results of the meta-analysis were largely unsupportive for cycle shifts in mate preferences. Specifically, fertile women did not particularly desire sex in short-term relationships with men purported to be of higher genetic quality. In the other meta-analysis, Gildersleeve and colleagues (2014a) analyzed a total sample of 50 reports from 38 published and 12 unpublished studies. This analysis concluded that ovulatory cycle effects are robust, not due to publication bias alone (as indicated by p-curve analysis; see Simonsohn, Nelson, & Simmons, 2014), and are confined to women's preferences for men in a purely sexual mating context. Cycle shifts were present when women evaluated men's "short-term" attractiveness and absent when women evaluated men's "long-term" attractiveness. Critically, this relationship only reached significance for body masculinity. Additionally, only partial support for facial masculinity was found (Gildersleeve et al. 2014a). Results from this meta-analysis further indicated no support for cycle shifts for facial symmetry and vocal masculinity (no statistical significance). The authors attributed these null effect to underpowered analyses.

Since then, the literature on cycle shifts in women's mate preferences received a lot of attention and more recent findings have mostly challenged the idea of the GGOSH. Some studies have already published null effects for cycle shifts in preferences before the opposing meta-analyses were published (Harris 2011; 2013; Peters, Simmons, & Rhodes, 2009), but a larger amount of studies were published within the following years. In particular, cycle shifts in preferences for masculine faces could not be replicated in several studies, some of which have been high-powered and longitudinal (Dixson et al., 2018; Jones et al., 2018a; Marcinkowska et al., 2016; Marcinkowska, Galbarczyk, & Jasienka, 2018; Muñoz-Reyes et al., 2014; Scott et al., 2014; Zietsch, Lee, Sherlock, & Jern, 2015). However, facial masculinity preferences were not the only preference dimension for which null replications were published. Two studies have also cast doubt on the robustness of preference shifts for masculine bodies (Marcinkowska et al., 2018; Peters et al., 2009). Despite these numerous null replications of possible cycle shifts in women's mate preferences for masculine faces or bodies, the literature still lacks of more recent, large-scale replication attempts for other previously published dimensions (e.g. voice masculinity, behavioral traits). One could argue that the cycle shift literature suffers from replication crisis (Open Science Collaboration, 2015), most likely as a consequence of varying methodological approaches.

1.4 Methodological problems

Methodological criticisms of the previous studies have been raised and might account for mixed findings. Sample sizes, participant scheduling and study design have often been insufficient and the conducted studies are characterized by a high methodological flexibility. In the following, I will explain the most prominent issues that have been highlighted in the literature. Most importantly, it is the combination of a number of problems that might have led to an overestimation of effect sizes and false positives.

1.4.1 "Researcher degrees of freedom"

"Researcher degrees of freedom" is a construct that was first named and explained by Simmons, Nelson and Simonsohn in 2011. It refers to "ambiguity of flexibility in data collection and analysis practices that enables researchers to try out several methods and, possibly, choose whichever method or analysis produces significant results, thereby dramatically increasing the Type 1 error rate" (Gildersleeve et al., 2014a, p.45). This problem does not only affect ovulatory cycle research, but is also a well-known issue in all scientific fields. The term "researcher degrees of freedom" has often been used with negative connotations, because it might have caused a large amount of false positive findings in the literature. However, originally, the term simply describes the fact that all researchers have to decide how to conduct their study, formulate their hypotheses, analyze their data and report their results, out of a number of different opportunities (Wicherts et al., 2016). Every choice can lead to different results, which might cause problems in replication attempts. This does not imply that authors of previous studies, which fail to be replicated, manipulated their results. It is simply a problem that one should be aware of when interpreting non-reproducible results.

1.4.2 Inappropriate sample sizes

Another explanation of mixed findings regarding cycle shifts is the relatively weak power in most previously reported studies (Gangestad et al., 2016; Jones et al., 2018a). Gildersleeve and colleagues (2014b) constructed p-curves of reported significant findings and found consistent p-curves with statistical power of only 33%. Gangestad and colleagues (2016) simulated more than 58,000 cycles based on published data to assess the validity of counting methods and recommend sample sizes that would be crucial to detect small, medium or large effects. For example, to achieve 80% power to detect a Cohen's *d* of 0.4 with backward counting (counting backward from next menstrual onset to assess conception probability) in between-subject designs, a sample size of 1,143 participants is recommended. An appropriate sample size to detect the same effect with the same power in a within-subject design would include at least 157 participants (assessed twice). Since forward counting

(counting forward from last menstrual onset to assess conception probability), a procedure that was used quite often, is seen as a less valid method, recommended sample sizes for this method are even higher (1,872 for between-subject and 258 for within-subject designs, respectively). Interestingly, effect sizes and sample sizes in reported studies were rather small (Gildersleeve et al., 2014a). For example, Jones and colleagues (2018a) reported that the mean sample size in within-subject studies showing significant fertile phase preference shifts for masculine faces was only 40 participants (median was 34 participants). Sample sizes in between-subject studies have been comparably small, indicating that the majority of studies cited as evidence for the GGOSH were underpowered. Therefore, previously reported effects might have been false positives or due to publication bias.

1.4.3 Between-subject designs

Previous studies often used between-subject designs to study changes across the ovulatory cycle, which clearly are within-subject effects (Gangestad et al., 2016). As already stated above, between-subject designs have a far lower statistical power than within-subject designs. Moreover, even when sample sizes are large, selection bias could confound any identified effects (Arslan et al., 2018). More precisely, observed between-subject effects might be due to differences between sampled women that are not due to changes across the cycle, such as diseases or different genetic makeups (Arslan et al., 2018). Indeed, Zietsch and colleagues (2015) reported that between-subjects variation in preferences for masculine faces is more accounted for by genes than by any other context-dependent factor (e.g. conception risk). Furthermore, because typical cycle length varies far more between women than within women (Cole, Ladner, & Byrn, 2009), and previous studies often sampled between women without scheduling them to a particular cycle phase, conception risk or cycle phase estimates might be especially unreliable in between-subject studies. These findings indicate that between-subject designs are unsuitable for detecting presumably subtle within-subject effects

(Arslan et al., 2018; Blake, Dixson, O'Dean, & Denson, 2016; Gangestad et al., 2016; Gonzales & Ferrer, 2016; Jones et al., 2018a). Nevertheless, Gonzales and Ferrer (2016) reported, that 62% of all cycle studies that were reviewed in the meta-analyses by Gildersleeve and colleagues (2014) as well as Wood and colleagues (2014) were actually between-subject studies.

1.4.4 Methodological flexibility in defining fertile windows

One problematic aspect that is more unique to cycle studies, is a high flexibility in estimating the fertile window. This flexibility in defining high-and low fertility windows has led to various, inconsistently used methods. First, in previous studies, there was no consistency in the length of estimated fertile days. Some studies used 3-day windows for high conception risk (e.g. Macrae, Alnwick, Milne, & Schloerscheidt, 2002), others ranged from 6 to 9 days (e.g. Harris, 2011; 2013; Penton-Voak & Perrett, 2000). Two studies even reported a 14-day (Penton-Voak et al., 1999) or a 20-day window for their analyses (Frost, 1994). Second, previous studies have often tried to standardize cycle lengths to the average value of 28 days, or even excluded participants with cycle lengths longer than 28 days from analyses (e.g. Little et al., 2007; Penton-Voak & Perrett, 2000). This happened although 28 days is just the average cycle length between women (Wilcox, Dunson, & Baird, 2000) and regular cycle lengths are often longer, with a length of 35 days still be seen as normal (Creinin, Leverline, & Meyn, 2004). Third, the majority of cycle phase estimates in the literature relied on self-report data (Wood et al., 2014). Women often fail to recall the day of their last menstrual onset and the accuracy of this report was shown to be as low as 57% (Wegienka & Baird, 2005), which produces a high error rate in cycle phase estimates. Fourth, most of the previous studies have used counting methods to assess conception probability (Gangestad et al., 2016). With the forward-counting method, ovulation is predicted to occur 14-15 days after menstrual onset, the backward-counting method estimates ovulation by subtracting 14 days from the next predicted menstrual onset (Blake et al., 2016). However, ovulatory cycle length fluctuates within- and between women, with the follicular phase (the phase between menstrual onset and ovulation) length being more variable than the luteal phase (the phase between ovulation and next menstrual onset) and, hence, forward counting producing more unreliable estimates (Arslan et al., 2018; Blake et al., 2016; Gangestad et al., 2016). Backwards counting, although slightly better than forward counting, might also lead to inaccurate estimates of the ovarian cycle phases (validity estimates range from .2 to .7 for correlations of estimated and actual fertility; Arslan et al., 2018). The most accurate, non-invasive method to validate fertile window estimates is a luteinizing hormone (LH) test, a relatively inexpensive hormonal measure of ovulation (Blake et al., 2016; Gangestad et al., 2016). Ovulation is expected to occur 24-48 hours after an LH-surge (Blake et al., 2016). However, although actually being the best method to pinpoint ovulation[2], LH tests have only been used in a minority of cycle studies (Cantú et al., 2014; Ditzen et al., 2017; Dixson et al., 2018; Marcinkowska et al., 2018).

1.4.5. Lack in direct hormone measures

Besides the fact that most studies did not use LH tests, only a few studies directly assessed ovarian hormone levels (see Ditzen et al., 2017; Feinberg et al., 2006; Jones et al., 2018; Marcinkowska et al., 2018; Pisanski et al., 2014; Roney & Simmons, 2008; Roney et al., 2011). This is important to note because measuring hormones is crucial to investigate the mechanisms potentially underlying cycle shifts, since women's ovulatory cycle is regulated by shifts in hormone concentrations. Ovarian hormone levels have sometimes been estimated based on cycle phase estimations by counting methods (Lukaszewski & Roney, 2009; Puts,

[2] Because of the fact that LH tests are more reliable in determining the day of ovulation than counting methods, studies including LH tests need much less participants to achieve a higher test power, compared to studies with counting methods. Based on test power simulations done by Gangestad and colleagues (2016), to achieve 80% power to detect an effect of d = .05, a within subject-study with forward counting would need 190 participants, with backward counting 71 participants, but only 48 participants when including LH tests. Needed sample sizes for between-subject studies to detect the same effect are up to ten times higher.

2006), which, as a matter of fact, is error-prone and much less reliable than direct assessments. However, most of the previous studies did not assess or estimate hormone levels at all.

1.4.6 Stimuli material with low ecological validity

Previous studies show a high variation in used stimuli material. Most studies used computer manipulated (e.g. morphed) faces, bodies or voices (e.g. Feinberg et al., 2006; Little et al., 2007; Marcinkowska et al., 2018; Penton-Voak et al., 1999; Pisanski et al., 2014; Puts, 2005), acted behavior (Cantú et al., 2014) and even drawn bodies (Pawlowski & Jasienka, 2005). Natural stimuli, for example videos of real behavior or unmanipulated stimuli have only been used in a few studies (Gangestad et al., 2004; 2007; Peters et al., 2009; Puts, 2006). It is up for debate to what degree computer-manipulated or drawn stimuli actually have ecological validity. In any case, natural stimuli should provide a high ecological validity and should be used to ensure that results can be transferred to real-life mate preferences.

1.5 Theoretical Conclusion

With this dissertation, I sought to contribute to the scientific discourse about the existence of ovulatory cycle shifts in women's mate preferences. For this purpose, my colleagues and I conducted a study investigating cycle shifts in preferences for three established dimensions: men's bodies, behaviors and voices. Reviewing the literature indicates that the evidence for cycle shifts is not as strong and congruent as previously assumed. Whereas the theoretical background of the GGOSH was well elaborated, a large number of methodological issues have been criticized so far. We wanted to prevent these problems by preregistering our approach, making our data available at the open science framework, employing a high-powered within-subject design and using state of the art methods. We validated fertile window estimates with LH tests, directly measured hormone levels and used natural stimuli. Additionally, we assessed women's relationship status and self-reported stress to test these variables as possible moderators of cycle shifts.

2. Summary of Manuscript 1

In the first manuscript, we investigated if women's mate preferences for men's bodies change across the ovulatory cycle. Previous studies reported mate preference changes for masculine body shape (Little et al., 2007), tall men (Pawlowski & Jasienka, 2005) and rated muscularity (Gangestad et al., 2007), but, as already stated above, there are many methodological points of criticism regarding the previous literature. Hence, the aim of this study was to test the GGOSH regarding proposed masculine characteristics in men's bodies.

A sample of 157 heterosexual, naturally cycling women took part in the study. All participants attended four lab testing sessions across two ovulatory cycles, two times in their fertile (late follicular) phase and two times in their luteal (non-fertile) phase. Cycle phases were first estimated via the backward counting method (Gildersleeve, Haselton, Larson, & Pillsworth, 2012) and then confirmed via LH tests. In every testing session, participants had to rate 80 male bodies of men in standardized underwear, captured with a 3D body scanner, on sexual- and long-term attractiveness. Steroid hormones were assessed via saliva samples. Contrary to previous findings, results indicated that men's masculine traits did not interact with women's cycle phase. Thus, no compelling evidence for specific ovulatory cycle shifts in women's mate preferences was shown. Rather, when fertile, women's ratings of men's bodies generally increased for sexual as well as for long-term attractiveness. Further analyses revealed that nearly every male body received higher ratings when evaluated fertile, regardless of masculinity. This attraction shift effect was only evident in partnered women and partially mediated by the estradiol-to-progesterone ratio. We found an additional partial mediator effect by lower estradiol levels on sexual attractiveness ratings. Self-reported stress did not moderate women's attraction shifts across the cycle. However, the effect disappeared when self-reported stress levels were high, suggesting that high stress overrides cycle effects on sexual attraction. In sum, women's mate preferences for masculine bodies seem to be stable across the ovulatory cycle, but their attraction for all male bodies (on average) shifts, mediated by estradiol and the estradiol-to-progesterone ratio. However, these shifts seem to be exclusive for women in relationships and can be suppressed by subjective perceived stress. These results are inconsistent with the GGOSH, yet might be correlated with higher general sexual desire in the fertile phase (as reported by Jones et al., 2018b).

3. Summary of Manuscript 2

In the second manuscript, our aim was to directly probe the GGOSH for men's behaviors. Preference shifts for men's dominant, masculine, or charismatic behavior were long seen as robust and the dimension with the strongest evidence for which cycle shifts could occur (Gangestad, 2017; Gildersleeve et al., 2014a). This was despite the fact that shifts like these have only been tested in a few studies with dissimilar investigated behaviors. These studies showed evidence for cycle shifts in preferences for men displaying behavioral dominance, confidence and social presence (Gangestad et al., 2004; 2007; Lukaszewski & Roney, 2009) and flirtatious facial movement (Morrison, Clark, Gralewski, Campbell, & Penton-Voak, 2010). Other studies showed evidence for changes in women's flirting behavior and behavioral engagement towards men with purported markers of genetic fitness (Cantú et al., 2014; Flowe, Swords, & Rockey, 2012). Nevertheless, again, criticism arose regarding methodological problems in these studies, just as for other studies that investigated ovulatory cycle shifts in preferences. Therefore, there is a strong need for replication with a high-powered, pre-registered design. We decided to investigate cycle shifts in preferences for men's flirting behavior, behavioral attractiveness and dominance or social presence related cues like self-display behaviors or speaking time. Flirting behavior was suggested to be done to exaggerate one's qualities as a mate (Back, Penke, Schmukle, Sachse, Borkenau, &

Asendorpf, 2011). Behavioral attractiveness may be a more indirect indicator than flirting behavior, but could also display men's efforts to appeal attractive towards women. Self-display behaviors have been seen as an attempt to impress the conversation partner, appear to index what would commonly be thought of as courtship-like behavior and are correlated with higher testosterone levels in men (Roney, Mahler, Maestripieri, 2003; Roney, Lukaszewski, & Simmons, 2007). Moreover, direct dominant behavior usually includes intrasexual competitions between men (Gangestad et al., 2004), which might not be as relevant as flirting in modern world mating situations.

All methods were the same as in Manuscript 1 (sample, procedure, measures, pre-registration), except for the used stimuli material. Instead of men's rotating bodies, all participants had to rate natural videos of 70 men in flirtatious dyadic interactions on sexual- and long-term attractiveness. In every video, a male participant was seated in a room with an attractive female confederate and they were instructed to get to know each other. In the next step, their behavior was rated by independent, trained raters (see Penke & Asendorpf, 2008 for details). In line with Manuscript 1, results revealed no compelling evidence for women's mate preferences shifts across the ovulatory cycle. Rather, we again found a robust main effect for shifts in women's attraction for potential sexual- and long-term partners that was only present for women in relationships. Shifts in women's sexual attraction were partially mediated by higher estradiol levels, whereas shifts in long-term attraction were partially mediated by a lower estradiol-to-progesterone ratio. Self-reported stress did not affect attractiveness ratings or cycle phase attraction shifts. In sum, we again did not find supporting evidence for the GGOSH, but higher mate attraction in the fertile phase for women in committed relationships.

4. Summary of Manuscript 3

In the third manuscript, we tested for evidence of cycle shifts in preferences for masculine voices. Previous studies have reported some evidence for preference shifts for masculinized voices, characterized by a lower voice pitch and lower, more closely spaced formant frequencies (Feinberg et al., 2006; Pisanski et al., 2014; Puts, 2005; 2006). Even though some of these studies failed to report significant effects, they interpreted their findings as evidence that preferences for masculine characteristics in men's voices are related to women's cycle phase. Lack of evidence for these shifts in a meta-analytical approach was attributed to underpowered analyses (Gildersleeve et al., 2014a). Once again, there is a strong need for high powered replication studies. For this purpose, we combined the datasets of two large, independent within-subject studies from different labs. In Study 1, 202 heterosexual, naturally cycling women were tested twice. One session was scheduled within their estimated fertile phase and one during their estimated luteal phase (via backward counting). In every session, participants rated the sexual attractiveness of voice recordings from six male voices, all manipulated (raised or lowered) in fundamental frequency (F_0; the acoustic measure closest to what we perceive as voice pitch) and formant dispersion (D_f; the average distance between consecutive formant frequencies computed across the 4 formants), resulting in four recordings per male voice. Main predictors of attractiveness ratings were women's directly measured estradiol and progesterone levels. Conception risk was also estimated via backward counting, assigned accordingly (as in Puts, 2005) and validated with progesterone levels. Sample and methods of Study 2 are the same as in Manuscript 1 and Manuscript 2, except for the stimuli material. For investigating cycle shifts in voice preferences, participants rated 76 natural voice recordings of different men, counting from three to eight. This stimuli material was recorded as part of the Berlin Speed Dating Study (see Asendorpf, Penke, & Back, 2011 for more information) and voice parameters were analyzed using Praat software (Boersma & Weenink, 2006).

We found no compelling evidence for ovulatory cycle shifts in women's mate preferences for masculine voices in both studies. Masculine vocal cues did not interact with estimated conception risk, cycle phase or ovarian hormone levels. Rather, in Study 2, we again found evidence suggesting an attraction shift towards all presented voices with higher sexual and long-term attractiveness ratings when women were fertile. However, Study 1 only provided partial evidence for this attraction shift, because estimated conception risk did not influence attractiveness ratings, whereas progesterone and the estradiol-to-progesterone ratio did in the majority of analyses. Nevertheless, we did not find a clear pattern of hormonal regulations of attraction shifts, because progesterone levels did, counter-intuitively, positively and robustly influence attractiveness ratings in Study 2. Our analyses did not reveal any effects of women's relationship status or self-reported stress. These results contrast with prior work on mate preference shifts for masculine voices, but mostly align with our findings reported in Manuscripts 1 and 2.

5. General Discussion

The question whether estrous mate preference shifts are robust is the subject of high controversy. It plays an important role in evolutionary psychological literature and was the leading question of my dissertation. To contribute to the scientific discourse about ovulatory cycle shifts in women's mate preferences, I tested the GGOSH for three different masculine dimensions: men's bodies, behaviors and voices. Besides that, I also tested cycle shifts in women's attraction, hormonal regulations of this effect and possible moderator variables. The results of the studies, reported in three manuscripts, do consistently show no compelling evidence for the GGOSH, thus, no preference shifts across the cycle. Rather, the results support the idea of a general shift in mate attraction, because women rated all men as slightly more attractive when fertile, partially mediated by ovarian hormones, regardless of men's physical or behavioral traits. Regarding evaluations of men's bodies and behaviors, this effect was only evident for women in relationships. Self-reported stress did suppress attractiveness ratings for men's bodies, but did only have a slight influence on ratings for voices, but none on behaviors. The main findings of the present studies are also displayed in Table 1. In the following sections, I will review the implications of these findings, discuss possible explanations, current limitations and possible questions for future research.

Table 1

Overview of the results from the three manuscripts

Observed evidence for…	Men's bodies (Manuscript 1)	Men's behaviors (Manuscript 2)	Men's voices (Manuscript 3 Study 1)	Men's voices (Manuscript 3 Study 2)
1) Preference shifts?	**No** *No interaction between cycle phase and masculine characteristics*	**No** *No interaction between cycle phase and behavioral traits*	**No** *No interaction between conception risk (or hormone levels) and masculine characteristics*	**No** *No interaction between cycle phase and masculine characteristics*
2) Attraction shifts?	**Yes** *Main effect for cycle phase on attractiveness ratings (sexual and long-term)*	**Yes** *Main effect for cycle phase on attractiveness ratings (sexual and long-term)*	**Partly** *Positive main effect for P and negative for E/P on attractiveness ratings, but not for conception risk*	**Yes** *Main effect for cycle phase on attractiveness ratings (sexual and long-term)*
3) Hormonal influences?	**Yes** *Attraction shift partially mediated by lower E* on sexual attractiveness; by higher E/P in both rating dimensions*	**Yes** *Main effect of E on sexual attractiveness, but also negative effect of E/P* on long-term attraction*	**Yes** *Positive main effect for E/P and negative for P on attractiveness ratings*	**Yes*** *Positive main effect of P* on both rating dimensions, negative effect of E/P* on long-term attraction*
4) Effects of relationship status?	**Yes** *Attraction shift only evident for partnered women*	**Yes** *Attraction shift only evident for partnered women*	**N/A** *Relationship status was not assessed in this study*	**No** *Attraction shift evident for singles and partnered women*
5) Effects of self-reported stress?	**Partly** *Stress overrides effects of cycle phase on sexual, but not long-term attraction*	**No** *No significant main effect of stress, no significant interaction effects*	**N/A** *Self-reported stress was not assessed in this study*	**Partly** *Negative main effect for stress, but no significant interaction with cycle phase*

Note. E = estradiol, P = progesterone, E/P = estradiol-to-progesterone ratio. *Marks effects that were "counter-intuitive" and in the opposite direction than theoretically assumed.

5.1 Cycle shifts in women's mate preferences

Comparable to other recent, high-powered longitudinal studies (Jones et al., 2018a; Marcinkowska et al., 2018), we did not find compelling evidence for ovulatory cycle shifts in women's mate preferences. When fertile, women did not selectively evaluate men with characteristics of proposed "good genes" as more attractive for sexual relationships. Moreover, results did not differ between evaluations for sexual and for long-term attractiveness. Our sample and methods differ from those in previous studies reporting evidence for preference shifts to a notable extent, which might have led to contradictory results. First, our sample was not only much larger than samples in previous studies, but it is also the first German sample (vs. samples from other countries, mostly from the US) with a higher mean age of participants compared to most other studies (notably, one exception is Manuscript 3, Study 1 with a sample originate from the US and a similar age span to previous studies). Second, we employed a within-subject design (vs. between-subjects designs), validated our cycle phase estimates using LH tests (vs. relying on forwards- or backwards counting methods only), directly measured ovarian hormones (vs. estimating hormone levels) and used natural stimuli (vs. artificially manipulated or drawn stimuli). Third, we preregistered our study, which reduced researcher degrees of freedom in conducting the study and analyzing our data.

As a matter of fact, studies that have reported evidence for the GGOSH contain different problems that might have led to overestimation of effect sizes and false positives. Nevertheless, two previously reported studies have used methodologically strong designs (Jones et al., 2018a; Marcinkowska et al., 2018; however, these studies used manipulated stimuli and did not preregister their approaches). Jones and colleagues (2018a) tested women's preferences for masculine faces in 351 naturally cycling participants across up to five test sessions. Marcinkowska and colleagues (2018) included 99 women in their within-subject analyses and investigated possible preference shifts for symmetrical or masculine faces as well as masculine bodies. Interestingly, both studies reported null effects and hence could not replicate evidence for the GGOSH. However, absence of evidence is not stringently evidence of absence and the fact that we did not find support for the GGOSH doesn't mean that preference shifts do not exist in general. For example, preference shifts for other domains (e.g. odor) might be robust and we don't know if preference shifts do only occur under specific conditions.

Concluding, I cannot finally clarify if cycle shifts in mate preferences exist[3], but if they do, they seem to be more complex than previously assumed and further research is needed to clarify under which specific conditions they are observable. Though, next to recent studies with appropriate designs, the results reported in this dissertation challenge the existing evidence for the GGOSH.

5.2 Cycle shifts in women's mate attraction

Rather than preference shifts, we reported a general attraction shift towards men across the ovulatory cycle in all three manuscripts. More precisely, in the fertile phase, nearly all men were evaluated as being more attractive than in the luteal phase, regardless of men's physical or behavioral traits. Interestingly, previous studies have already shown some initial evidence for attraction shifts and observed a main effect of cycle phase or conception risk on attractiveness ratings (e.g. Dixson et al., 2018; Gangestad et al., 2004; 2007). This effect has not been interpreted before, mainly because interpretations were focused on the GGOSH and this main effect was usually seen as qualified by an interaction of cycle phase and masculine

[3] I do not discuss the hormonal pattern of preference shifts or influences of women's relationship status and self-reported stress, as we did not find compelling evidence for the occurrence of preference shifts. Nevertheless, we directly investigated hormonal influences on possible preference shifts and did not observe any significant effects. Importantly, we also analyzed possible three-way interactions between cycle phase, relationship status and masculine cues. Again, these analyses did not reveal any evidence for preference shifts (or influences of women's relationship status on preference shifts).

cues. In contrast, I suggest this general fertile phase increase in women's attraction to men to be connected to fertile phase increases in sexual motivation and desire. Other studies have already reported evidence for an increase of general sexual desire (Jones et al., 2018b; Roney & Simmons, 2013) or in-pair as well as extra-pair desire (Arslan et al., 2018; Roney & Simmons, 2016) in women's fertile phase, which support this assumption. However, this connection between sexual desire and mate attraction needs further investigation.

Notably, the effect sizes we observed for attraction shifts were rather small. Therefore, previous studies using smaller sample sizes or between-subject designs may have not been able to detect this effect due to their lower test power. This might also be the reason why we did not find evidence for an effect of conception risk on attractiveness ratings in Study 1 of Manuscript 3 (with n = 51 tested twice). Additionally, the attraction shift effect disappeared in some of our robustness checks in Manuscript 3. Hence, more research is needed to investigate if this effect is stable, under which circumstances it occurs and, if the relationship between cycle phase and mate attraction is mediated by sexual desire.

5.2.1 Hormonal patterns of attraction shifts

Shifts in sexual desire across the cycle were reported to be regulated by ovarian hormonal changes. Jones and colleagues (2018b) reported negative effects of progesterone and positive effects of estradiol on different facets of sexual desire, whereas testosterone and cortisol levels did not affect perceived general sexual desire. These findings are in line with those reported by Roney and Simmons (2013; 2016). If attraction shifts and sexual desire are connected, they should have comparable hormonal influences. However, our results of hormonal predictors for cycle shifts in attraction were rather unclear. Indeed, in line with the findings on sexual desire, we did not find evidence for effects of testosterone or cortisol on ratings in all three manuscripts. Additionally, we observed a positive partial mediator effect of estradiol on sexual attractiveness ratings for behaviors (Manuscripts 2) as well as a negative effect of progesterone on voice attractiveness ratings (Manuscript 3, Study 1). Also in line with this, we found a partial positive mediator effect of the estradiol-to-progesterone ratio on sexual and long-term attractiveness ratings for masculine bodies (Manuscript 1) and a generally positive estradiol-to-progesterone ratio effect on voice attractiveness ratings (Manuscript 3, Study 1). Nonetheless, we did also find hormonal effects that do not align with findings of previous work: negative effects of the estradiol-to-progesterone ratio on long-term attractiveness ratings of behaviors and voices (Manuscript 2; Manuscript 3, Study 2), as well as a negative partial mediator effect of estradiol on masculine bodies (Manuscript 1) and positive influences of progesterone on sexual attractiveness ratings of voices (Manuscript 3, Study 2). Hence, although the majority of our observed effects align with the findings of hormonal influences on sexual desire, some of them do not follow a clear pattern. These results arise two questions about hormonal influences on attraction shifts that lead to directions for future research.

a) *What are possible explanations for this inconclusive pattern and different hormonal effects in the three manuscripts?* Since hormonal influences are different on specific facets of sexual desire (Jones et al., 2018b), one idea is that they also vary between sexual desire and attraction, which might explain why we did not find the same hormonal influences as those predicting sexual desire (Jones et al., 2018b; Roney & Simmons, 2013; 2016). Furthermore, it is also possible that they even vary for different masculine cues or stimuli material (e.g. voices, faces, bodies). However, this would still not explain the contradictory effects of progesterone on evaluated voice attractiveness in Manuscript 3, Study 1 (negative effect) and Study 2 (positive effect). Given the large number of analyses across all manuscripts and the fact that the positive effect of progesterone does not align with theoretical assumptions as well as findings of previous work, this effect might also be a false positive. Therefore, I suggest that this finding has to be replicated in advance to further interpretation.

b) *Why are cycle shifts in women's attraction not fully explainable by hormonal changes?* Although cycle shifts are expected to be regulated by hormonal changes across the cycle, we only found partial mediator effects or even no mediator effects of hormones at all. There are different possible explanations for these findings. First, there might be a temporal delay in the effect of estradiol on desire and, hence, mate attraction. For example, Roney and Simmons (2013) reported that women's levels of sexual desire were positively predicted by estradiol levels measured two days earlier, whereas measured estradiol on the same day only yielded a descriptive but non-significant effect. Since we did not assess hormone samples two days prior to the testing sessions, we were not able to test whether attraction shifts were fully mediated by delayed effects of hormone levels. Second, there might be other important, probably more social variables that influence attraction shifts. For example, it was reported that sexual desire varies systematically across weekdays, with higher levels of desire on weekends compared to all other weekdays, independent of hormone concentrations (Roney & Simmons, 2013; 2016; but see Arslan et al., 2018). Moreover, Roney (2017) argues that women's relationship status might be another non-hormonal variable that influences women's sexual desire and motivations. How being in a committed relationship vs. being single, as well as subjective perceived stress levels might influence attraction shifts, will be explained in the next chapter.

5.2.2 Women's relationship status and self-reported stress

We reported evidence, that women's relationship status might be an important variable that influences women's attraction to men. Comparable evidence from sexual desire research already shows that women's mating psychology might be generally sensitive to the presence or absence of a stable investing partner. More precisely, when a supporting long-term partner is absent, the costs of pregnancy might outweigh its' benefits (Pillsworth, Haselton, & Buss, 2004). Furthermore, women's sexual desire has been reported to be generally higher in early stages of relationships and to decrease over time (Dennerstein, Lehert, and Burger, 2005; Murray & Millhausen, 2012; Pillsworth et al., 2004). Moreover, there is evidence that feelings for a current partner are strong positive predictors of sexual motivation, an effect that remained stable after controlling for hormonal influences on desire (Dennerstein et al., 2005). Additionally, there is opposing evidence on the assumption that women's relationship status does not only moderate the strength of sexual motivation, but might even trigger it. On the one hand, it has been reported that only partnered women, not singles, showed increased fertile phase sexual desire (Pillsworth et al., 2004; Roney & Simmons, 2016). On the other hand, Jones and colleagues (2018b) found no compelling evidence that hormonally driven shifts in women's general sexual desire were moderated by their relationship status, which speaks against the assumption that hormonal and non-hormonal variables might have additive effects on sexual desire (as suggested by Roney, 2017).

The results reported in this dissertation reflect this unclear pattern of influences of women's relationship status on desire and, thus, possibly connected mate attraction. On the one hand, attraction shifts for men's bodies or behaviors were only observed for partnered women, not for singles (descriptively, singles also rated men's bodies as more attractive in the fertile phase, but this effect was not significant). On the other hand, attraction shifts for men's voices were equally observed for singles and partnered women. There is no empirical evidence that explains differences in these results so far. Possibly, visual stimuli (e.g. bodies and videos of interacting situations) might trigger responses dissimilarly than vocal stimuli do, potentially because of the diverging hormonal effects we observed between ratings of the different stimuli. Beyond that, effect size estimates of the attraction shift effects were rather small and test power might still have been too low to detect attraction effects for single women (about half of the sample) regarding bodies and behaviors. Alternatively, the observed attraction effect for single women in Manuscript 3 might also be a false positive. However, since the effects of relationship status on psychological changes across the ovulatory cycle remain unclear, future research should a) replicate these findings and b) if replicable, investigate why the influence of women's relationship status differs among attraction to specific masculine characteristics.

In previous research, psychological stress was also suggested to negatively influence mate preferences (Ditzen et al., 2017) or ovarian hormone levels (Roney & Simmons, 2015), but overall evidence is rather scarce. We did not observe a clear pattern regarding influences of stress on mate attraction. Our results indicate that self-reported stress does not moderate attraction shifts, but it suppresses sexual attraction for men's bodies and has a negative effect on voice attractiveness ratings (which is somehow in line with results reported by Ditzen and colleagues, 2017 as well as Roney and Simmons, 2015). However, self-reported stress did not have any effects on attractiveness ratings for men's behaviors. Moreover, cortisol levels, which are assumed to reflect stress levels (e.g. Burke, Davis, Otte, & Mohr, 2005), did not influence attractiveness ratings. Given the possibility that we did not assess subjective stress levels appropriately (see "limitations") and the fact that these results do not indicate a clear pattern, I recommend further investigations rather than interpreting the current findings.

5.3 Alternative theories

The literature provides alternative theories to the GGOSH that describe how ovarian hormones could influence mate attraction and preferences. Subsequently, I will interpret if the results reported in this dissertation can serve as preliminary support for the most prominent alternative theories. Though, it has to be acknowledged that my primary aim was to test the GGOSH and my study design does not allow a full valid test of the other hypotheses. Hence, these interpretations should be treated with caution.

5.3.1 The "perceptual spandrel" hypothesis

The "perceptual spandrel[4] hypothesis" primarily describes differences in women's physical attractiveness across the cycle. However, it also proposes that variability in women's mate preferences might be a by-product of between-women differences in hormone levels (Havliček, Cobey, Barrett, Klapilová, & Roberts, 2015). According to this theory, shifts in women's mate preferences are hormonally mediated, especially by estradiol levels. Women with higher estradiol levels should possess a higher mate value, because they are generally evaluated as being more attractive than women with lower estradiol levels (after controlling for BMI; Grillot, Simmons, Lukaszewski, & Roney, 2014; but see Jones et al., 2018c). Hence, when estradiol rises in women's fertile phase, they should be perceived or feel as being more attractive and, due to assortative mating[5], also prefer more attractive men as partners. Women with relatively lower estradiol levels should perceive higher cyclical variation in their mate preferences than women with relatively higher estradiol levels (because of a "ceiling" effect; Havliček et al., 2015). There might be comparable effects for progesterone or testosterone. The hypothesis explicitly predicts no systematic differences between partnered or single women, as well as between sexual and long-term attractiveness ratings (Havliček et al., 2015). We did, indeed, not observe any systematical differences between sexual and long-term ratings, but differences in ratings between partnered and single women for men's bodies and behaviors. However, higher estradiol levels only predicted attraction shifts for men's behaviors, but not for voices. The effect of estradiol on men's bodies was even in a negative direction. Most importantly, we did not observe any preference shifts at all, neither across the cycle, nor in any interactions between estradiol, progesterone or testosterone and masculine cues. Hence, this hypothesis does not seem to be supported by our findings.

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[4] A spandrel is defined as „an inevitable by-product of the development of another adaptive trait, without itself being a direct product of selection" (Havliček et al., 2015, p. 1249).

[5] Active positive assortative mating would be to mate with a person who is as attractive as oneself (e.g. Todd, Penke, Fasolo, & Lenton, 2007).

5.3.2 Between-cycle effects

Rather than shifting within-cycles, women's mate preferences or attraction might shift between cycles, depending on the overall estradiol concentration (Roney, 2009). More precisely, women might experience shifts in attraction or preferences in cycles with higher estradiol levels, because such cycles might be on average "more fertile" with a higher probability of conception (Lipson & Ellison, 1996; Lukaszewski & Roney, 2009; Roney & Simmons, 2013). Evidence for this theory would indicate preference or attraction shifts that are predicted by estradiol levels alone (Lukaszewski & Roney, 2009). Although we found some evidence that estradiol influenced attractiveness ratings of men's bodies and behaviors, higher ratings were not fully mediated by estradiol levels. Moreover, women's ratings of men's voices were not predicted by estradiol levels at all. These results indicate that women's attraction to men is not fully dependent on their estradiol concentration alone, but might also be explained by other factors that are not predicted by the between-cycles theory.

5.3.3 Motivational priority shifts

Based on life history theory, women's motivations might change across the cycle: When women can conceive, their mating motivations (e.g. sexual interests) have a greater priority because the probability of conception provides a fitness benefit that outweighs potential costs of sex (Roney, 2017; Roney & Simmons, 2017). Other motivations (e.g. motivation to forage and eat) receive less priority in the fertile phase, but more during cycle phases when women cannot conceive (e.g. the luteal phase). Ovarian hormones, especially estradiol and progesterone, should regulate shifts of opposite effects on feeding and sexual motivation (Roney, 2017). In line with this assumption, recent research found increases in women's sexual desire and interests in their fertile phase (Arslan et al., 2018; Jones et al., 2018b; Roney & Simmons, 2013; 2016), as well as a higher food-intake in women's non-conceptive luteal phase (Roney & Simmons, 2017). These changes in women's motivations across the cycle were regulated by estradiol and progesterone levels (Roney & Simmons, 2013; 2016; 2017).

We were not able to directly test tradeoffs between women's sexual motivation and food intake, because we did not assess women's motivations to eat. However, the attraction shift we observed might be an indirect indicator of a higher mating motivation when fertile, in line with the motivational priority shifts theory. Nevertheless, this theory also predicts that fluctuating hormone concentrations, especially estradiol and progesterone, will produce changes in motivational priorities. Yet, we did not observe a consistent association between hormone levels and attraction shifts, but we found at least partial evidence for effects of estradiol, progesterone and the estradiol-to-progesterone ratio on attractiveness ratings. Although our evidence is not fully convincing, it might be interpreted as preliminary support for this theory.

5.4 Limitations

Although the studies reported in this dissertation had a number of strengths compared to previous studies, I also note some limitations that should be addressed in future research. First, previous studies that have provided evidence for cycle phase shifts in preferences for men's behaviors were assessing behaviors more directly related to dominance and social presence within an intrasexual competitive context. In contrast, we used ratings of flirting behavior, behavioral attractiveness and self-display behavior. It is possible that the behaviors assessed in competitive contexts (e.g. Gangestad et al., 2004; 2007) were better indicators of good genes, because they implied a willingness to risk confrontations with other men, whereas simply flirting with women while same-sex rivals are absent, may not carry similar implications. However, dominance or social presence might be traits that are somewhat stable across situations. Hence, for example, a man who behaves dominantly in intrasexual competitive situations, might also show more dominant behavior in flirting situations.

Nevertheless, it remains unclear if preference shifts would be observable if women have watched and evaluated an intrasexual competitive scene between two men, rather than a flirting context.

Second, women's self-reported stress levels were assessed in an accompanying online diary study with a planned missing design. Due to this design, the relevant stress item was only shown on about 40% of all days, therefore, not always capturing the same day as the assessed attractiveness ratings. Furthermore, for self-reported stress analyses, out of 157 participants, we lost 54 for both cycles, and 62 for one cycle, because they did not fill out the diary study regularly. This circumstance dramatically reduced our test power, resulting in an available dataset of only 160 cycles (out of 314 possible cycles) for these analyses. Future research should rather assess stress ratings within the testing sessions to ensure to capture stress levels at the respective days.

6. Conclusion

In this dissertation, I sought to clarify whether women experience mate preference and attraction shifts across the ovulatory cycle. In the reported studies, we intended to overcome methodological problems of previous studies by using substantially larger datasets, robust methods of fertility estimations and preregistered our approach. We did not observe any mate preference shifts across the ovulatory cycle, but found evidence for general mate attraction shifts, that might be connected to sexual desire and may support a motivational priority theory rather than the GGOSH. However, future research is needed to prove the hormonal basis of attraction shifts as well as non-hormonal influences, such as women's relationship status and self-reported stress. We do not know yet whether preference shifts for other domains (e.g. odor) are robust or if preference shifts only occur under specific conditions. However, in this dissertation, I was able to show that preference shifts across the ovulatory cycle are more complex than previously assumed. Moreover, this dissertation provided first evidence for mate attraction shifts across the cycle. Although not all observed patterns lead to a clear picture, they offer a number of directions for further research and contribute to the understanding of hormonal and non-hormonal influences on women's mating psychology.

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Appendix A.

Manuscript 1

Jünger, J., Kordsmeyer, T. L., Gerlach, T. M., & Penke, L. (2018). Fertile women evaluate male bodies as more attractive, regardless of masculinity. *Evolution and Human Behavior*, *39*, 412-423. DOI: 10.1016/j.evolhumbehav.2018.03.007

Supplementary material and open data are available at https://osf.io/n4hj6/

Fertile women evaluate male bodies as more attractive, regardless of masculinity

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Declaration of interest: The authors declare that they have no conflict of interest.

Abstract

Ovulatory cycle shifts in women's mate preferences have been documented for several physical and behavioral traits. Research suggests that, at peak fertility, women tend to prefer men with characteristics that reflect good genes for short-term sexual relationships. However, existing findings have been criticized for methodological flexibility and failing attempts to replicate core results. In a large (*N*=157), pre-registered, within-subject study spanning two ovulatory cycles, we investigated cycle shifts in women's mate preferences for masculine bodies. Using a large set of natural stimuli, we found that when fertile, women's ratings of male bodies increased for sexual as well as for long-term attractiveness. Both effects were partially mediated by the estradiol-to-progesterone-ratio. Furthermore, moderation analyses revealed that both shifts were only evident in women in relationships, but not in singles. Contrary to previous findings, male masculine traits did not interact with cycle phase to predict attraction, indicating that women's preferential priorities do not shift. Taken together, our results do not support women's mate preference shifts, as assumed by the good genes ovulatory shift hypothesis, but are consistent with shifting motivational priorities throughout the cycle. Implications of these results for female estrus theories and methodological recommendations for future research are discussed.

Keywords: ovulatory cycle, mate preferences, body masculinity, steroid hormones, fertility, attractiveness

Introduction

The existence of systematic changes in women's mate preferences across the ovulatory cycle has been discussed widely in the evolutionary sciences. There is evidence that naturally cycling women in their fertile phase, compared to their luteal phase, evaluate masculine stimuli as more attractive for short-term relationships (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Gildersleeve, Haselton, & Fales, 2014a). However, recent research casts doubts on these results (Gangestad et al., 2016; Wood, Kressel, Joshie, & Louie, 2014). Whereas there are already some researchers debating if ovulatory shifts in women's preferences for masculine faces, voices or odor exist (e.g. Feinberg et al., 2006; Harris 2011; 2013; Peters, Simmons, & Rhodes, 2009; Thornhill, Chapman, & Gangestad, 2013), surprisingly little research focused on possible preference changes for masculine bodies. Therefore, the present study aims to clarify whether women experience such systematic shifts across the ovulatory cycle and whether these shifts are regulated by changes in steroid hormones or moderated by women's relationship status or self-reported stress levels.

Many non-human mammals show estrus behavior during ovulation, and their fertile phase is the only time when they are sexually receptive or proceptive. In rats, cats, cattle, and sheep, female behavioral changes and sexual activity is mediated by changes in ovarian hormones (Dixson, 2012; Feder, 1981). Moreover, females of many non-human primate species change their mate preferences across the ovulatory cycle: When fertile, they mate more selectively, choosing high-quality males, likely to enhance their own and their offspring's survival and fitness (Matsumo-Oda, 1999; Pieta, 2008; Stumpf & Boesch, 2005).

Unlike other primates, human females appear equally sexually receptive throughout the whole ovulatory cycle. However, they experience similar changes in ovarian hormones and their sexual interests vary across the cycle (Arslan, Schilling, Gerlach, & Penke, 2017; Gangestad, Thornhill, & Garver, 2002; Gangestad, Thornhill, & Garver-Apgar, 2005;

Haselton & Gangestad, 2006; Roney & Simmons, 2013; 2016). This raises the question if women may also, homologous to some non-human primate species, experience ovulatory cycle shifts regarding their mate preferences. Whether human estrus exists and what its implications for women's mate choice are is still controversially debated in the literature. The most popular hypothesis regarding changes in women's mate preferences across the ovulatory cycle is the good genes ovulatory shift hypothesis (Arslan, et al., 2017; Gangestad et al., 2005). It states that human females change their mate preferences systematically across the ovulatory cycle and this may have evolved to facilitate a flexible mixed mating strategy in order to increase females' reproductive fitness. Accordingly, on fertile days, women should be sexually attracted to characteristics in men that reflect high genetic quality, compared to their none-fertile days (Gildersleeve et al., 2014a). These preference shifts should only be present in the context of short-term sexual relationships. For long-term relationships, women should put higher value on mates with a high potential and willingness to provide parental effort and these long-term preferences should not vary across the ovulatory cycle (Gildersleeve et al., 2014a; Thornhill & Gangestad, 2015).

There are some masculine traits in men that are particularly assumed to reflect men's genetic quality. Masculine men have sometimes been found to show higher circulating testosterone levels (Penton-Voak & Chen, 2004, but see Kandrik et al., 2017; Scott et al., 2014 for contradictory evidence), which might make them an indicator of superior immune functioning in line with the immunocompetence handicap hypothesis (Hamilton & Zuk, 1982). Moreover, taller men have higher reproductive success (Mueller & Mazur, 2001; Nettle, 2002; Pawlowski, Dunbar, & Lipowicz, 2000, but see Stulp & Barrett, 2016) and indicators of physical strength could attract mates (Sell, Lukaszewski, & Townsley, 2017) because strength increases success in competing with other men and might therefore be a cue of male protection abilities (Hill et al., 2013; Kordsmeyer, Hunt, Puts, Ostner, & Penke, 2017; Sell et al., 2012). Furthermore, masculine characteristics in general have been linked to men's success in attracting mates (Gildersleeve et al., 2014a). Therefore, masculinity is argued to be a good indicator for genetic quality in men and should be a good variable to investigate possible cycle shifts in women's mate preferences. Previous studies have already found evidence for cycle shifts for masculine *faces* (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), *voices* (Feinberg et al., 2006; Puts, 2005) and *odor* (Gangestad & Thornhill, 1998; Havlíček, Roberts, & Flegr, 2005; Thornhill et al., 2013), apparently supporting the good genes ovulatory shift hypothesis. However, recent research casts doubt on this evidence, particularly because of several studies reporting null effects (e.g., Peters et al., 2009; Gangestad et al. 2016) and diverging conclusions from two recent meta-analyses on ovulatory cycle shifts (Gildersleeve et al., 2014a; Wood et al., 2014) lead to a considerable debate (Gangestad & Haselton, 2015; Gildersleeve, Haselton, & Fales, 2014b; Harris, Pashler, & Mickes, 2014; Hyde & Salk, 2014; Jones, 2014; Wood & Carden, 2014; Wood et al., 2014; Wood, 2015). In particular, cycle shifts in preferences for masculine faces could not be replicated in recent studies (Harris, 2011; 2013; Jones et al., in press a; Marcinkowska, Galbarczyk, & Jasienka, 2018; Munoz-Reyes et al., 2014; Peters et al., 2009; Scott et al., 2014).

The difficulty to replicate previous findings on cycle shifts in mate preferences could at least in part be ascribed to three issues evident in many earlier studies: low statistical power, methodological flexibility, and lack of hormone assessments. In many previous studies, sample sizes have likely been too small and interindividual (instead of intraindividual) comparisons have made it even more difficult to achieve appropriate statistical power (Gangestad et al., 2016). Moreover, across those studies, women's cycle phase was estimated with varying methods (Harris, 2011). Urine tests, which measure the luteinizing hormone (LH) to pinpoint ovulation, have often been missing (Gangestad et al., 2016). Finally, while changes in women's mate preferences should be regulated by changes in steroid hormones, almost all of the above referenced studies lacked direct assessments of these hormones (but see Marcinkowska et al., 2018; Jones et al., in press a). In sum, the exact association between ovulatory cycle shifts in women's mate preferences and changes in steroid hormones remains unclear. Additional evidence that clarifies the current scientific discourse with multiple hormone assessments throughout the cycle is needed.

Only few studies so far have focused on masculine *bodies*, which is surprising, since human bodies are highly sexually dimorphic. Masculinity, as a purported indicator of good genes, is probably best identifiable in body characteristics. In particular, only three studies have demonstrated that women's preferences for men's masculine body traits may change across the ovulatory cycle: during their fertile phase, women showed an increase in mate preferences for tall men (Pawlowski & Jasienka, 2005), masculine body shape (Little, Jones, & Burriss, 2007), and rated muscularity (Gangestad et al., 2007). In contrast, two studies did not find evidence for ovulatory cycle shifts in preferences for body masculinity (Marcinkowska et al., 2018; Peters et al., 2009). Notably, all these studies used artificial stimuli (e.g., drawn or morphed), which might not mirror real world instantiations of body masculinity and its range (but see Gangestad et al., 2007). In addition, these studies either had relatively small sample sizes for both female participants (but see Gangestad et al., 2007) and male stimuli, conducted interindividual (instead of intraindividual) comparisons (but see Marcinkowska et al., 2018; Peters et al., 2009), or did not measure hormones (but see Marcinkowska et al., 2018). Measuring hormones, however, is crucial to pinpoint the mechanisms potentially underlying ovulatory cycle shifts. If preference shifts are indeed regulated by changes in steroid hormones, they should be mediated by changes in estradiol and progesterone (Jones et al., 2005; Jones et al., in press a; Puts, 2006; Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011), as the fertile phase of the cycle prior to ovulation is characterized by higher levels of estradiol and lower levels of progesterone (Gangestad & Haselton, 2015; Puts et al., 2013). In contrast, levels of estradiol are lower and levels of progesterone are higher during the luteal phase, when conception risk is low. However, the analysis of estradiol, progesterone and the estradiol-to-progesterone-ratio (E/P ratio) might not be sufficient. Recent research suggests that psychological stress and the hormone cortisol should also be measured. Stress was found to induce higher cortisol levels (Herrera, Nielsen & Mather, 2016), sometimes inhibiting estradiol emission in young women (Roney & Simmons, 2015) and decrease women's preferences for male facial masculinity (Ditzen, Palm-Fischbacher, Gossweiler, Stucky, & Ehlert, 2017 but see Jones et al., in press a). Therefore, women's stress level might affect their mate preferences across the ovulatory cycle and should be investigated as a possible moderator. Furthermore, another hormone that might influence ovulatory cycle shifts is testosterone, which varies slightly but systematically across the cycle (e.g. Puts, 2006; Roney & Simmons, 2013). In recent studies, it was shown that women's preferences for masculine faces are strongest when testosterone levels are relatively high (Welling et al., 2007) and that early follicular testosterone correlates positively with preferences for men's facial masculinity (Bobst, Sauter, Foppa, & Lobmaier, 2013). These results indicate that testosterone may potentially also play a role in masculinity preference shifts across the cycle.

While steroid hormones may be the underlying physiological mechanism, to get a more complete picture of the processes underlying ovulatory cycle shifts, other variables should be taken into account. One such variable might be women's relationship status. According to the dual mating strategy hypothesis (Pillsworth & Haselton, 2006) based on the strategic pluralism model (Gangestad & Simpson, 2000), women may receive fitness benefits when forming a relationship with a reliable investing man, while seeking good genes from another man through extra-pair sexual encounters. Studies found that at peak fertility women are more likely to have sexual fantasies about men other than their primary partner (Gangestad et al., 2002), while reporting more commitment to their primary partner in the luteal phase compared to the late follicular phase (Jones et al., 2005). There is also evidence for cycle shifts in general sexual desire among partnered women that did not occur for singles

(Roney & Simmons, 2016). In addition, normally cycling women in committed relationships have been found to report stronger masculinity preferences than singles (Jones et al., in press a) and to rate the odor of dominant men as sexy, whereas singles did not (Havlíček et al., 2005). Therefore, women's relationship status could be a moderator of cycle shifts in mate preferences and should be investigated in greater detail.

Overview of the current study

In the current study, we aim to clarify a) whether there are mate preference shifts for masculine male body characteristics across the ovulatory cycle, b) which hormonal changes might underlie these shifts and c) which moderators influence these shifts. By employing a pre-registered study design with a large sample size and multiple assessment of steroid hormones across two ovulatory cycles, we directly addressed criticism of cycle effect studies recently raised in the literature. In particular, in our study, women's fertile phase was not only estimated via forward- and backward counting methods, but was also validated with the use of urine tests measuring the luteinizing hormone. In addition, instead of just estimating the levels of ovarian hormones according to the calculated conception risk, they were directly assessed in women´s saliva. Hormones such as cortisol and testosterone, which have only infrequently been investigated in previous research, were analyzed as possible mediator variables in an exploratory manner. To increase ecological validity in the assessment of women's masculinity preferences, we used natural, unmanipulated 3D stimuli, which avoid potentially unnatural characteristics or exaggerating effects in artificially manipulated stimuli. A large set of stimuli were presented to increase reliability. Masculinity indicators were measured directly from the stimulus men in order to test if cycle shifts lead to stronger preferences for natural body masculinity and to explore which aspects of body masculinity are most important in that regard. Finally, possible moderating influences of women's relationship status and self-reported stress were investigated.

Hypotheses and Research Questions

All hypotheses tested in the current manuscript are part of a pre-registration[1]. Following previous findings on ovulatory cycle shifts in mate preferences, we hypothesized that women in the fertile phase, as compared to their luteal phase, evaluate masculine bodies as more attractive for short-term relationships (Hypothesis 1). This effect should be mediated by increases in estradiol and decreases in progesterone (Hypothesis 2). Following the good genes ovulatory shift hypothesis, women in their fertile phase should be more sexually attracted to men with indicators of high genetic quality, compared to low-fertility days of their cycle (Gangestad et al., 2005; Gildersleeve et al., 2014a). Therefore we also pre-registered the hypothesis that shifts in short-term mate preferences are shown for men with the visual cues of upper-body strength (shoulder-chest ratio, shoulder-hip ratio, upper-torso volume relative to lower-torso volume, upper arm circumference) and taller body height. Additionally, shifts in short-term mate preferences could also be shown for men with higher testosterone levels (which has been assumed to coordinate all kinds of visible masculinity cues) and higher physical strength (Hypothesis 3a). It should be noted that, contrary to the other body characteristics measured directly from the body scans, testosterone and strength do not constitute directly visible cues. Still, both can be assumed to be linked to morphological cues visible in the body stimuli (e.g. Bhasin, 2003; Pound, Penton-Voak, & Surridge, 2009), but potentially not captured by the other measures. Therefore, we included them here as indirect cues. We predict our findings to be robust when controlling for the possible confounding variables age and body mass index (BMI). Because of the ongoing debate about whether or not cycle shifts in preferences for masculine characteristics exist, we also pre-registered the alternative hypothesis that naturally cycling women in their fertile phase, compared to their luteal phase, do not differ in their evaluations of masculine stimuli's attractiveness for short-term relationships

[1] This pre-registration also contained further hypotheses that are not part of the present paper.

(Hypothesis 3b). One possible moderator for these cycle shifts might be women's relationship status. Since it remains unclear if single and partnered women both pursue different mating strategies across the cycle, we state two alternative hypotheses: Cycle phase shifts in preferences for short-term mates are larger for partnered women than for single women (as predicted by the strategic pluralism model, Gangestad & Simpson, 2000; Hypothesis 4a), or, alternatively, relationship status does not affect the strength of cycle shifts in preferences for short-term mates (Hypothesis 4b). Because recent research suggests that psychological stress inhibits estradiol concentrations in young women (Roney & Simmons, 2015), we hypothesize self-reported stress as a moderator for occurring cycle shifts: Cycle shifts should be attenuated when self-reported stress is high (Hypothesis 5). In accordance with the good genes ovulatory shift hypothesis, we also hypothesized that preference shifts should be absent or only weakly present when it comes to long-term mate preferences (Hypothesis 6; Gildersleeve et al., 2014a).

Material and Methods

Our hypotheses, the study design, the sampling and the analysis plan had been pre-registered online at the Open Science Framework (https://osf.io/egjwv/) before any data have been collected or analyzed. All participants signed a written consent and the ethics committee of the Institute of Psychology at the University of Goettingen approved the protocol (no. 144).

Participants and Recruitment

Out of 180 recruited participants, 157 heterosexual female participants (aged 18-35, $M = 23.3$, $SD = 3.4$) finished all sessions and were therefore included in further analyses. Seventeen women who only attended the introductory session of the study dropped out before participation (six fulfilled one of the exclusion criteria below, four quit the study without further reasons, four did not respond to emails, three had scheduling problems). Another six dropped out during the study because they only completed the first testing session (four had scheduling problems, two did not respond to emails after the first session). Based on the inclusion criteria of other ovulatory cycle studies, our participants had to fit to the following preregistered criteria: female, between 18 and 30 years old [2], naturally cycling (no hormonal contraception for at least three months, no expected switch to hormonal contraception during the study, no current pregnancy or breastfeeding, no birth-giving or breast-feeding during the previous three months, not taking hormone-based medication or anti-depressants). Additionally, they had to report that their ovulatory cycles had a regular length between 25 and 35 days during the last 3 months. At the beginning of the study, 75 of the participants reported to be in a relationship, 82 reported to be single. By completion of all sessions, participants received a payment of 80€ or course credit, and a 3D printed figure of themselves.

Procedure

All participants took part in five individually scheduled sessions. In the first introductory session the participants received detailed information about the general procedure, duration of the study and compensation. Furthermore, the experimenter explained the ovulation tests and checked the inclusion criteria. To count the days to the next ovulation and to plan the dates of the experimental sessions, cycle length as well as the dates of the last and the next menstrual onset were assessed. Finally, demographic data was collected.

Sessions two to five, the computer-based testing sessions, took place across two ovulatory cycles per participant, once per cycle during the fertile and once during the luteal phase. To control for possible effects of diurnal changes in hormone levels (Bao et al., 2003; Veldhuis et al., 1988), all sessions took place in the second half of the day (mainly between 11.30 am and 6 pm). When arriving at the lab, participants first completed a screening questionnaire, assessing their eligibility and some control variables for the saliva samples (Schultheiss & Stanton, 2009). Next, the saliva samples were collected via passive drool

[2] One of the participants reported to be 35 years old. We included her data because she met all other including criteria and had positive LH-tests. Excluding her data did not change the results.

before the participants started their first rating task[3]. In their first testing session, all participants then saw a short preview video, presenting all male bodies they were about to evaluate for one second each, to avoid biased ratings resulting from not being familiar with the attractiveness range of all bodies. Furthermore, they were instructed to evaluate the men's attractiveness as they perceived it in that moment, independent of their current relationship status or general interest in other men.

Participants were then presented with the stimuli in a randomized order. The bodies were displayed rotating around their vertical axis, allowing them to be inspected from every side. To avoid the influence of confounding variables like facial attractiveness or skin color, the bodies were consistently colored in grey, without texture or head (see Figure 1). Thereby the stimuli contained information on body morphology only. Participants rated each stimulus after at least one full rotation, but were able to inspect them for as long as they preferred. Every stimulus was rated separately for sexual attractiveness (assessing short-term attraction) and for attractiveness as a long-term relationship partner on an eleven-point Likert scale from -5 (extremely unattractive) to +5 (extremely attractive), including zero as a neutral point. Definitions of sexual attractiveness and attractiveness for a long-term relationship were provided prior to the ratings and read as follows:

a) *Sexually attractive*: Men that score high would be very attractive for a sexual relationship that can be short-lived and must not contain any other commitment. Men scoring low would be very unattractive for a sexual relationship.
b) *Attractive for a long-term partnership*: Men that score high would be very attractive for a committed relationship with a long-term perspective. Men that score low would be very unattractive as a long-term partner.

[3]The described study on ovulatory cycle shifts for body masculinity was one part of a larger study (see pre-registration). Participants also had to complete other rating tasks and anthropometric data was collected between these tasks. The duration of one testing session was approximately 2-2.5h.

After each session, the appointment for the next session was arranged individually based on participant's ovulatory cycle.

Furthermore, all participants of the current study were asked to participate in a separate daily online diary study (Arslan, Jünger, Gerlach, Ostner, & Penke, 2016) that was conducted in parallel to the described lab study. Within this diary study, participants had to fill out a questionnaire about daily feelings and behavior across 70 days. We used the stress ratings from this study for further analyses (see below for more details).

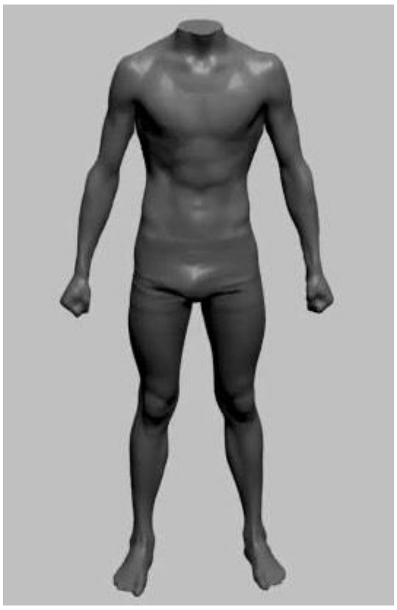

Figure 1. Static example of a 3D male body stimulus.

Measures

Ovulatory cycle phase

Women's cycle phase was determined by the reverse cycle day method, based on the estimated day of the next menstrual onset (Gildersleeve, Haselton, Larson, & Pillsworth, 2012) and confirmed by highly sensitive (10 mIU/ml) urine ovulation test strips from purbay®, which measure the luteinizing hormone (LH). These LH-tests had to be done at home at the estimated day of ovulation and the four days prior to that and results were self-reported by the participants. The study investigated two ovulatory cycles in which every participant reported to the lab twice: Once while being fertile (at the days prior to ovulation, usually reverse cycle day 16-18, with reverse cycle day 16 as the most ideal date) and once when not fertile (during the luteal phase, after ovulation and prior to the next menstrual onset, usually reverse cycle day 4-11, with reverse cycle days 6 to 8 as the most ideal dates). An Excel sheet was used to compute the acceptable days for the testing sessions and to track whether a participant started in her fertile or luteal phase. Of all participants who finished all sessions, 66 participants started with the first session in their luteal phase, 91 started in the fertile phase.

Stimuli and Masculinity Measures

Eighty male bodies, collected in an independent study (Kordsmeyer et al., 2017; Kordsmeyer & Penke, 2017), were presented. All stimuli were natural male bodies of men in standardized underwear (tight shorts), captured with a high-resolution 3D body scanner (Vitus Smart XXL by Human Solutions). Men were instructed to stand upright with legs hip-width apart, arms extended and held slightly away from the body, making a fist with thumbs showing forward, the head positioned in accordance with the Frankfort Horizontal, and to breathe normally during the scanning process. Body models were scaled so that they retained original height differences. Since we did not find any differences in attractiveness ratings between presenting the bodies life-sized via beamer on a white wall or on a computer screen in a pretest[4], we decided to present the stimuli on computer screens. Out of the 165 available bodies, we preselected stimuli based on adequate scan quality (12) and avoided missing values on target men's data (40). Among the remaining ones, selection of 80 suitable stimuli occurred at random. Visual cues of upper body strength were directly measured from the body

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[4]Between-subject design. Stimuli were divided in two sets (76 bodies per set) to avoid raters' tiredness, resulting in 15 rater per condition per set. All bodies were rated on eleven point Likert scales from -5 ("extremely unattractive") to +5 ("extremely attractive"). Comparisons between the ratings of all bodies revealed no significant differences between both conditions (presenting the stimuli on a computer screen vs. life-sized via beamer; $N = 60$, $M_{Computer} = -0.15$, $SD_{Computer} = 0.59$, $M_{Beamer} = 0.05$, $SD_{Beamer} = 0.66$, $t\ (58) = -1.25$, $p = 0.22$). Moreover, the attractiveness ratings in both conditions correlated highly ($r = 0.94$, $p = <.001$).

scans using the automatic measures of the software Anthroscan (all according to ISO 20685:2005), including the following parameters relevant to this study: bust-chest girth (Anthroscan measure 4510), hip girth (7520), upper arm girth (8520). In addition to automatic measurements, biacromial shoulder width was measured manually (on screen) as the direct distance between the left and right acromion processes. The volume (in liters) of upper torso and lower torso was also measured from scans. We calculated shoulder-chest ratio, shoulder-hip ratio and the relative volume of upper torso to lower torso. Physical strength was operationalized as the aggregated mean of men's dominant hand grip (88.2% used their right hand) and upper body strength, measured with a hand dynamometer (Saehan SH5001), following the procedure described in Sell, Cosmides, Tooby, Sznycer, von Rueden and Gurven (2009). The maximum strength of three trials for each measurement was used. Height was measured with a statiometer. To measure men's testosterone levels, saliva samples were taken across two afternoon testing sessions under resting conditions and analyzed via immunoassays (see Kordsmeyer et al., 2017). The values were averaged and log transformed.

Descriptive statistics for attractiveness ratings and masculinity measures of all men used as stimuli are shown in Table 1. To investigate the validity of the chosen stimuli, we analyzed attractiveness ratings from an independent sample of participants (60 female raters) in a pretest (interrater agreement was high, $\alpha = .92$). Pretest ratings correlated negatively with stimuli men's BMI ($r = -.30$, $p = .01$) and waist-to-hip-ratio ($r = -.46$, $p < .001$). They correlated positively with chest-to-waist-ratio ($r = .58$, $p < .001$), as well as facial attractiveness ($r = .26$, $p = .02$), rated by another independent sample of 12 female raters from standardized photographs. The latter correlation confirms the one ornament hypothesis, which proposes correlated attractiveness of faces and bodies (Thornhill & Grammer, 1999).

Table 1

Descriptive statistics of male stimuli characteristics and the ratings for short-term sexual attractiveness (ST) and long-term attractiveness (LT)

	M	*SD*	*min*	*max*
Age	24.09	3.33	18.00	34.00
Height (cm)	180.11	7.38	160.50	202.00
Weight (kg)	75.21	11.49	52.70	109.80
BMI	23.19	2.53	17.06	33.49
Strength (kg)	48.48	7.85	31.00	69.00
SCR	0.39	0.02	0.35	0.46
SHR	0.40	0.02	0.34	0.44
Attractiveness Rating ST	-0.36	2.78	-5.00	5.00
Attractiveness Rating LT	-0.32	2.77	-5.00	5.00

Note. BMI = Body mass index, SCR = shoulder chest ratio, SHR = shoulder hip ratio, ST = short-term sexual attractiveness, LT = long-term attractiveness. Attractiveness rating scales ranged from -5 to +5.

Hormone measures

For hormone assays, we collected four saliva samples from each participant (one per testing session). Contamination of saliva samples was minimized by asking participants to abstain from eating, drinking (except plain water), smoking, chewing gum or brushing teeth for at least one hour before each session. The samples were stored at -80°C directly after collection until shipment on dry ice to the Kirschbaum Lab at Technical University of Dresden, Germany, where estradiol, progesterone, testosterone and cortisol was assessed via liquid chromatography mass spectrometry (LCMS; Gao, Stalder, & Kirschbaum, 2015). Since the LCMS analysis of the estradiol levels did only detect 22% of all possible values, the samples were reanalyzed using the highly sensitive 17β-estradiol enzyme immunoassay kit (IBL International, Hamburg, Germany). These latter estradiol values were used in subsequent analyses. We centered all hormone values on their subject-specific means and scaled them afterwards (i.e. divided them by a constant), so that the majority of the distribution for each hormone varied from -0.5 to 0.5 to facilitate calculations in the linear mixed models (as in Jones et al., in press a; b; c). This is a common procedure to isolate effects of within-subject changes in hormones, avoiding the influence of outliers on results and dealing with the non-normal distribution of hormone levels. Hormone levels were nearly normally distributed afterwards, a figure showing the distribution of hormone levels after this procedure can be found in the supplement (Figure S1). Importantly, this procedure did not change any findings compared to analyses with untransformed hormone values. The R code for this procedure can be found in the open script.

Stress ratings

Self-reported stress was measured via one item ("*Today I was stressed out*") on a five point Likert-scale (from "*less than usual*" to "*more than usual*") on a daily basis within the accompanying online diary study (see above) with planned missings[5]. For the analysis, the respective stress value of the same day of the lab testing session was taken. If there was no existing value for that day, we averaged the values of the two days before and after the testing day, if available. In total, 54 of the 157 participants were excluded from analyses, 26 because they did not take part in the diary study at all, 20 because they did not fill out enough days to get at least data for one fertile and one luteal session, eight because they took part in the study at another time window (not parallel to the lab study). Sixty-two participants filled out enough days for at least one fertile and one luteal session, 41 filled out enough days to analyze both fertile and both luteal sessions, resulting in an available dataset of 160 cycles (out of 314 possible cycles) in total.

Statistical analyses

All analyses were calculated with the statistic software R 3.4.0 (R Core Team, 2016). The following packages were used: lme4 1.1-13 (Bates, Maechler, Bolker, & Walker, 2014), lmerTest 2.0-33 (Kuznetsova, Brockhoff, & Christensen, 2013), ggplot2 2.2.1 (Wickham, 2009), psych 1.7.5 (Revelle, 2016), dplyr (Wickham, 2011).

[5] The participants had to fill out more than 100 items per day. Therefore, we decided to reduce the daily items by planned missings to avoid too much dropouts, but still get enough data for every item. The relevant stress item was shown on about 40% of all days.

Results

Preliminary Analyses

First, we counted how many cycles were reported as being irregular (more than three days deviation between testing session and a-priori defined windows of appropriate testing days; see section "ovulatory cycle phase"). Even though all participants reported to have regular ovulatory cycles in the introductory session, eight women reported irregularity in both investigated cycles, 32 reported one cycle being irregular, resulting in 48 out of 314 (15.3%) cycles being irregular. Next we checked how many of the participants' ovulatory cycles had positive LH tests (indicating a LH surge) in the calculated fertile phase to detect non-ovulatory cycles. Twelve participants reported negative LH test results for both investigated cycles, nine reported negative LH tests results for one cycle. In total, the LH tests in 33 of all 314 cycles (10.5%) were negative. Additionally, we checked the temporal relationship between the reported day of LH surge and the date of scheduled testing session. Because ovulation usually occurs within 24-36 hours after the observed LH surge, testing sessions that were scheduled more than two days after the surge might have already been in the early luteal phase. Out of the 281 cycles for which an LH surge was observed, thirteen (4.63%) purportedly fertile phase sessions were scheduled three or four days after the LH surge. Therefore, 268 (95.37%) were scheduled within an appropriate range of three days before to two days after the LH surge (in total: M = -0.12, SD = 1.39 days in relation to the day of the observed LH surge). A histogram showing the distribution of days of fertile phase testing sessions relative to the observed LH surge can be found in the supplement (Figure S2). Participants with irregular cycles, negative LH-tests or the risk of early luteal phase instead of fertile phase testing session were still included in the main analyses, but excluded in robustness checks.

Ovulatory cycle shifts in women's mate preferences for body masculinity

First we tested whether there were ovulatory cycle shifts in women's attractiveness ratings for male bodies, independent from men's masculinity characteristics (Hypotheses 1 and 6). For multilevel analyses, we included attractiveness ratings as dependent variable (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness), a random intercept per female rater as well as for male stimulus, and women's cycle phase (0 = luteal phase, 1 = fertile phase) as a fixed effect. This analysis showed a significant cycle shift in women's attraction: When fertile, ratings for sexual attractiveness were higher than in the luteal phase of the ovulatory cycle ($\gamma = 0.07$, $SE = 0.02$, $t = 4.44$, $p < .001$, $95\%CI = [0.04; 0.11]$), supporting Hypothesis 1. Similar results were found for the long-term attractiveness ratings ($\gamma = 0.09$, $SE = 0.02$, $t = 4.83$, $p < .001$, $95\%CI = [0.05; 0.12]$), contrary to Hypothesis 3. Figure 2 shows how women's attraction changes as a function of cycle phase. These results indicate the existence of ovulatory cycle shifts on women's mate attraction to male bodies, independent of the relationship condition (sexual- vs. long-term), such that, in general, fertile women rated males' bodies as being more attractive.

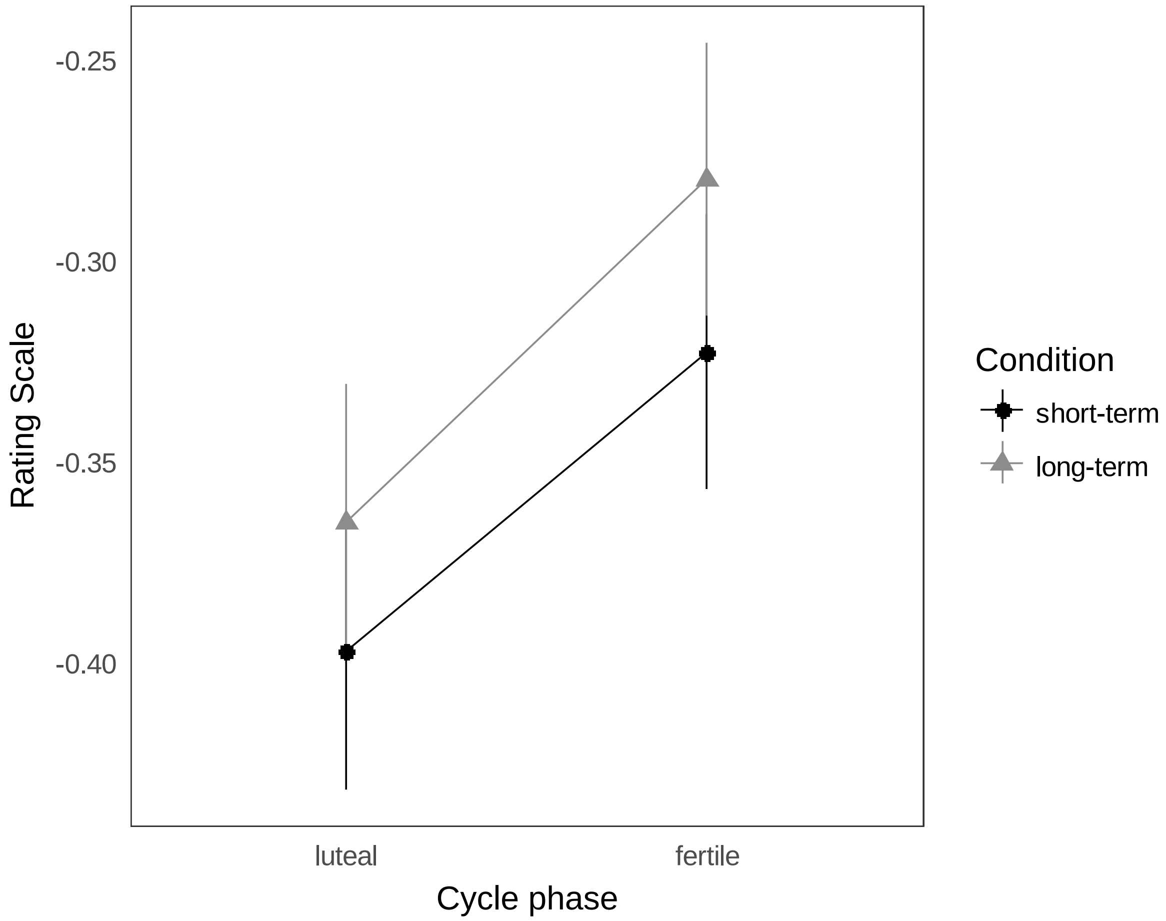

Figure 2. Averaged attractiveness ratings for short-term (measured as sexual attractiveness) and long-term relationships in function of women's cycle phase. Rating scale ranged from -5 to +5, the Y-axis is truncated. Error bars represent 95% confidence intervals.

Second, we tested if participants showed preference shifts across the ovulatory cycle for specific body characteristics that reflect masculinity (Hypotheses 3a, 3b and 6). Again, female raters as well as the male stimuli were treated as random effects. Women's cycle phase and men's masculine characteristics were treated as fixed effects[6]. Men's baseline testosterone levels, body height, physical strength, shoulder-chest ratio (SCR), shoulder-hip ratio (SHR), upper torso volume relative to lower torso volume and upper arm circumference were analyzed as masculine traits. Two separate analyses were run for a) sexual attractiveness and b) long-term attractiveness as dependent variables. The values of all men's masculine traits were z-standardized in order to place all on the same scale and to ease interpretation of

[6] Separate models for all cues revealed comparable results.

regression coefficients (γ). Multilevel within-subjects comparisons across two ovulatory cycles again showed significant cycle shifts for women's attraction in sexual as well as long-term attractiveness. In their fertile phase, women rated male bodies as more attractive for both relationship conditions, but none of the masculine traits interacted with cycle phase. Table 2 reports the results of the multilevel analyses of cycle phase and men's masculine traits for sexual attractiveness ratings. For ratings of long-term attractiveness, the results were similar (Table 3). Significant effects were found for cycle phase and physical strength, whereas all interactions between cycle phase and masculine characteristics remained non-significant. These results again support Hypothesis 1 and contradict Hypothesis 6. All effects for cycle phase and strength remained significant when controlling for men's age and BMI. However, there were significant main effects of men's BMI when including the control variables in the mixed effect model (sexual: $\gamma = -1.11$, $SE = 0.31$, $t = -3.59$, $p < .001$, $95\%CI = [-1.68; -0.54]$; long-term: $\gamma = -1.03$, $SE = 0.28$, $t = -3.71$, $p < .001$, $95\%CI = [-1.55; -0.51]$), as well as for men's age (sexual: $\gamma = -0.14$, $SE = 0.06$, $t = -2.38$, $p = .02$, $95\%CI = [-0.25; -0.03]$; long-term: $\gamma = -0.13$, $SE = 0.05$, $t = -2.44$, $p = .02$, $95\%CI = [-0.23; -0.03]$). These results indicate an absence of ovulatory cycle shifts in preferences for any masculine characteristic, contradicting Hypothesis 3a, but supporting Hypothesis 3b. Women rated men's attractiveness as higher in their fertile phase, compared to their luteal phase, regardless of masculinity. However, women showed preferences for strong men, younger men, and men with a lower BMI, but independent of cycle phase. All results were comparable across both attraction outcomes (sexual and long-term attractiveness).

As cycle shift in women's attraction were not driven by shifts towards stronger preferences for men with more masculine bodies, we further analyzed rating differences between fertile and luteal phase ratings. A very high Spearman rank correlation between sexual attractiveness ratings of the fertile and the luteal phase ($r = 0.998$, $p < .001$) indicated that the rank order of the most attractive to the most unattractive body was virtually identical in fertile and luteal phases. When looking at the differences in ratings between the fertile and the luteal phase, we found that most of the bodies (82.5%) received slightly better ratings in the fertile phase ($M_{fertile}$ = -0.32, *SD*= 1.77; M_{luteal} = -0.4, *SD* = 1.8; *d* = 0.04), even the least attractive ones. Long-term attractiveness ratings showed similar results: The Spearman-rank correlation between fertile and luteal phase ($r = 0.997$, $p < .001$) indicated hardly any rank order changes from the most attractive to the least attractive bodies. Again, most of the bodies (78.8%) received a better rating in the fertile phase compared to the luteal phase ($M_{fertile}$ = -0.28, *SD*= 1.57; M_{luteal} = -0.37, *SD* = 1.62; *d* = 0.06). These results show that women consistently evaluate all men's bodies as more attractive when they are in their fertile phase, leaving virtually no room for differential effects of masculinity cues.

Table 2

Results of multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase and men's masculinity cues

	γ	*SE*	*t*	*p*	*95% CI*
Women's cycle phase	0.07	0.02	4.44	<.001	[0.04, 0.11]
Men's baseline testosterone level	-0.02	0.22	-0.10	.92	[-0.44, 0.39]
Men's body height	-0.11	0.25	-0.43	.67	[-0.57, 0.36]
Men's physical strength	0.60	0.26	2.34	.02	[0.12, 1.09]
Men's SCR	-0.03	0.28	-0.11	.91	[-0.57, 0.50]
Men's SHR	0.34	0.30	1.12	.26	[-0.23, 0.91]
Men's upper-torso volume (relative to lower-torso volume)	-0.16	0.23	-0.73	.47	[-0.59, 0.26]
Men's upper arm circumference	-0.33	0.27	-0.12	.22	[-0.83, 0.18]
Cycle phase x men's baseline testosterone level	0.02	0.02	0.81	.42	[-0.02, 0.05]
Cycle phase x men's body height	0.03	0.02	1.31	.19	[-0.01, 0.07]
Cycle phase x men's physical strength	-0.00	0.02	-0.11	.91	[-0.05, 0.04]
Cycle phase x men's SCR	-0.00	0.02	-0.10	.92	[-0.05, 0.04]
Cycle phase x men's SHR	0.00	0.03	0.11	.91	[-0.05, 0.05]
Cycle phase x men's upper torso volume	0.01	0.02	0.75	.46	[-0.02, 0.05]
Cycle phase x men's upper arm circumference	-0.02	0.02	-0.72	.47	[-0.06, 0.03]

Note. Women's cycle phase, men's masculine traits and their interactions as predictors for sexual attractiveness ratings. All variables had 50,240 observations (157 participants x 4 test sessions x 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All values were z-standardized.

Table 3

Results of multilevel regression analyses of long-term attractiveness ratings as a function of cycle phase and men's masculinity cues

	γ	*SE*	*t*	*p*	*95% CI*
Women's cycle phase	0.09	0.02	4.83	<.001	[0.05, 0.12]
Men's baseline testosterone level	-0.03	0.20	-0.13	.90	[-0.40, 0.35]
Men's body height	-0.04	0.22	-0.20	.84	[-0.47, 0.38]
Men's physical strength	0.47	0.23	2.00	<.05	[0.03, 0.90]
Men's SCR	0.01	0.26	0.03	.98	[-0.48, 0.49]
Men's SHR	0.28	0.27	1.01	.32	[-0.24, 0.79]
Men's upper-torso volume (relative to lower-torso volume)	-0.21	0.20	-1.02	.31	[-0.59, 0.18]
Men's upper arm circumference	-0.30	0.24	-1.25	.22	[-0.76, 0.15]
Cycle phase x men's baseline testosterone level	0.02	0.02	0.84	.40	[-0.02, 0.05]
Cycle phase x men's body height	0.02	0.02	0.97	.33	[-0.02, 0.06]
Cycle phase x men's physical strength	-0.00	0.02	-0.03	.97	[-0.05, 0.04]
Cycle phase x men's SCR	0.02	0.03	0.64	.52	[-0.03, 0.07]
Cycle phase x men's SHR	-0.01	0.03	-0.53	.60	[-0.07, 0.04]
Cycle phase x men's upper torso volume	0.01	0.02	0.58	.56	[-0.03, 0.05]
Cycle phase x men's upper arm circumference	-0.02	0.02	-0.70	.49	[-0.06, 0.03]

Note. Women's cycle phase, men's masculine traits and their interactions as predictors for long-term attractiveness ratings. All variables had 50,240 observations (157 participants x 4 test sessions x 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All values were z-standardized.

Steroid hormones as possible mediators

In order to analyze whether steroid hormones mediate effects of cycle phase (Hypothesis 2), estradiol, progesterone, testosterone, cortisol and estradiol-to-progesterone ratio (E/P ratio) were entered in the multilevel model. Results depicted in Table 4 demonstrate that for both attractiveness ratings, the E/P ratio partially mediated the effect of cycle phase on attractiveness ratings. Ratings were higher when the E/P ratio was high (i.e., in the fertile phase of the ovulatory cycle), the effect for cycle phase decreased, but stayed significant, partially supporting Hypothesis 2. We found additional partial mediator effects for estradiol, progesterone and cortisol, in that sexual attractiveness ratings were higher when estradiol and cortisol levels were lower, while long-term attractiveness ratings were higher when progesterone was high. Again the effect for cycle phase decreased in both cases, but stayed significant. All other measured hormones did not have any significant effects on the attractiveness ratings. However, our decision to include the E/P ratio in the same model with estradiol and progesterone might have caused collinearity problems. Therefore, we additionally calculated separate models with estradiol, progesterone, testosterone and cortisol as fixed effects, but excluding E/P ratio, for sexual as well as long-term attractiveness ratings. Results remained virtually identical, besides the former negative effect of cortisol on sexual- and the positive effect of progesterone on long-term attractiveness ratings that slightly failed to reach significance (Table 5). However, the effect sizes for all effects did not change noticeably.

Table 4

Multilevel regression analyses of attractiveness ratings as a function of cycle phase and hormone levels as possible mediator variables

	γ	*SE*	*t*	*p*	*95% CI*
Sexual					
Cycle phase	0.07	0.02	3.26	<.01	[0.03; 0.12]
Estradiol	-0.10	0.03	-3.14	<.01	[-0.17; -0.04]
Progesterone	0.03	0.03	1.05	.30	[-0.03; 0.08]
E/P	0.05	0.02	2.39	.02	[0.01; 0.09]
Testosterone	0.01	0.01	0.90	.37	[-0.01; 0.04]
Cortisol	-0.06	0.03	-2.07	.04	[-0.11; -0.00]
Long-term					
Cycle phase	0.10	0.02	4.13	<.001	[0.05; 0.15]
Estradiol	-0.05	0.03	-1.40	.16	[-0.12; 0.02]
Progesterone	0.07	0.03	2.20	.03	[0.01; 0.12]
E/P	0.05	0.02	2.48	.01	[0.01; 0.10]
Testosterone	0.02	0.01	1.24	.21	[-0.01; 0.04]
Cortisol	-0.02	0.03	-0.73	.47	[-0.08; 0.04]

Note. All variables had 42,720 observations (157 participants x 4 test sessions x 80 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All hormone values were centered to their subject-specific means and then scaled.

Table 5

Multilevel regression analyses of attractiveness ratings as a function of cycle phase and hormone levels as possible mediator variables, excluding the E/P-ratio

	γ	*SE*	*t*	*p*	*95% CI*
Sexual					
Cycle phase	0.09	0.02	4.08	<.001	[0.05; 0.13]
Estradiol	-0.08	0.03	-2.59	<.01	[-0.14; -0.02]
Progesterone	0.02	0.03	0.77	.44	[-0.03; 0.08]
Testosterone	0.01	0.01	0.78	.44	[-0.02; 0.04]
Cortisol	-0.05	0.03	-1.80	.07	[-0.10; 0.00]
Long-term					
Cycle phase	0.12	0.02	5.01	<.001	[0.07; 0.16]
Estradiol	-0.03	0.03	-0.76	.45	[-0.09; 0.04]
Progesterone	0.06	0.03	1.92	.06	[-0.00; 0.11]
Testosterone	0.02	0.01	1.12	.26	[-0.01; 0.04]
Cortisol	-0.01	0.03	-0.43	.67	[-0.07; 0.04]

Note. All variables had 42,720 observations (157 participants x 4 test sessions x 80 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All hormone values were centered to their subject-specific means and then scaled.

Relationship status

To test if women's current relationship status moderated the ovulatory cycle shifts in their mate attraction (Hypothesis 4a and 4b), we first classified all women who reported to be in an open relationship[7], in a committed relationship, engaged, or married as in a relationship. During the study, the relationship status changed for 13 participants. Their data was categorized in accordance with their relationship status on the particular testing day. We again calculated a multilevel mixed regression model with female rater and male stimuli as random effects, women's cycle phase and their relationship status were treated as fixed effects. As shown in Table 6, there was a significant interaction between cycle phase and relationship status, but no significant main effects. To closer investigate this interaction effect, we analyzed ratings from partnered women vs. singles separately. Results displayed in Table 7 indicate that only partnered women showed cycle shifts and rated men's bodies as more

[7] We additionally analyzed the data by classifying women who reported to be in an open relationship as singles, which did not change any results notably.

attractive when they were fertile. The results were similar for sexual- and for long-term relationships and support Hypothesis 4a, but not 4b.

Table 6

Multilevel regression analyses of attractiveness ratings as a function of cycle phase and women's relationship status

	γ	*SE*	*t*	*p*	*95% CI*
Sexual					
Cycle phase	0.01	0.02	0.56	.57	[-0.03; 0.06]
Relationship status	0.09	0.06	1.37	.17	[-0.04; 0.21]
Cycle phase x Relationship status	0.12	0.03	3.68	<.001	[0.06; 0.19]
Long-term					
Cycle phase	0.03	0.02	1.26	.21	[-0.02; 0.08]
Relationship status	-0.06	0.07	-0.97	.33	[-0.19; 0.07]
Cycle phase x Relationship status	0.11	0.04	3.20	.001	[0.04; 0.18]

Note. All variables had 50,240 observations (157 participants x 4 test sessions x 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile, and relationship status with 0 = single, 1 = in a relationship.

Table 7

Multilevel regression analyses of attractiveness ratings as a function of cycle phase with separate analyses for partnered vs. single women

	γ	*SE*	*t*	*p*	*95% CI*
Sexual: Partnered women					
Cycle phase	0.14	0.02	5.77	<.001	[0.09; 0.19]
Sexual: Single women					
Cycle phase	0.01	0.02	0.62	.54	[-0.03; 0.06]
Long-term: Partnered women					
Cycle phase	0.14	0.03	5.56	<.001	[0.09; 0.19]
Long-term: Single women					
Cycle phase	0.03	0.02	1.28	.20	[-0.02; 0.08]

Note. Models for partnered women had 24,000 observations, models for single women had 26,240 observations. We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile.

Self-reported stress

Furthermore, we analyzed whether self-reported stress moderated the relationship between cycle phase and attractiveness ratings (Hypothesis 5). We calculated two further multilevel models (Model 1 for sexual-, Model 2 for long-term attractiveness ratings). Again, female raters as well as the male stimuli were treated as random effects. Women's cycle phase and self-reported stress ratings were treated as fixed effects. Since many women did not fill out the self-reported stress item for every testing day due to the planned missings design (see Methods), data for only about half of the sample (25,600 observations, $n = 103$ who completed minimum one cycle) was available. For sexual attractiveness ratings as outcome, we found a main effect of self-reported stress ($\gamma = -0.06$, $SE = 0.02$, $t = -2.97$, $p < .01$, *95%CI* = [-0.10; -0.02]), revealing that sexual attractiveness ratings were higher when self-reported stress was lower. The main effect of cycle phase ($\gamma = 0.03$, $SE = 0.06$, $t = 0.55$, $p = 0.58$, *95%CI* = [-0.8; 0.14]) and the interaction between cycle phase and self-reported stress were not significant ($\gamma = 0.03$, $SE = 0.03$, $t = 1.18$, $p = .24$, *95%CI* = [-0.02; 0.08]). For long-term ratings as outcomes, we found a main effect of cycle phase ($\gamma = 0.14$, $SE = 0.06$, $t = 2.44$, $p = .01$, *95%CI* = [0.03; 0.26]), showing that attractiveness ratings were higher in the fertile phase. The main effect of self-reported stress ($\gamma = -0.03$, $SE = 0.02$, $t = -1.44$, $p = 0.15$, *95%CI* = [-0.07; 0.01]) and the interaction between cycle phase and self-reported stress were not significant ($\gamma = -0.02$, $SE = 0.03$, $t = -0.76$, $p = .45$, *95%CI* = [-0.07; 0.03]). For both sexual- and long-term attractiveness, cycle phase and self-reported stress did not interact, indicating that there was no moderation effect of self-reported stress on cycle effects. These results contradict Hypothesis 5, but suggest that high stress overrides any cycle effects on sexual attraction.

Robustness checks

We conducted further analyses to test the robustness of our effects. To rule out that our results might have been caused by order effects of testing sessions (in particular participating in the first session when fertile; Suschinsky, Bossio, & Chivers, 2014), we controlled for type of first phase in our analyses. For both sexual- and long-term attraction the effect of cycle phase remained stable (sexual: $\gamma = 0.07$, $SE = 0.02$, $t = 4.44$, $p < .001$, *95%CI* = [0.04; 0.11]; long-term: $\gamma = 0.09$, $SE = 0.02$, $t = 4.83$, $p < .001$, *95%CI* = [0.05; 0.12]). Starting fertile vs. luteal did not affect the attractiveness ratings (sexual: $\gamma = -0.04$, $SE = 0.13$, $t = -0.33$, $p = .74$, *95%CI* = [-0.30; 0.21]; long-term: $\gamma = -0.17$, $SE = 0.14$, $t = -1.19$, $p = .24$, *95%CI* = [-0.44; 0.11]). Next, we added a variable for values of the first vs. the second tested ovulatory cycle as fixed effect to our basic model with cycle phase as another fixed effect, female raters and male stimuli as random slopes, to see if there were differences in ratings. For sexual- as well as for long-term relationships, the effects of cycle phase remained stable (sexual: $\gamma = 0.07$, $SE = 0.02$, $t = 4.45$, $p < .001$, *95%CI* = [0.04; 0.11]; long-term: $\gamma = 0.09$, $SE = 0.02$, $t = 4.85$, $p < .001$, *95%CI* = [0.05; 0.12]), but the attractiveness ratings were significantly higher in the first cycle across all participants (sexual: $\gamma = -0.31$, $SE = 0.02$, $t = -18.62$, $p < .001$, *95%CI* = [-0.34; -0.28]; long-term: $\gamma = -0.38$, $SE = 0.02$, $t = -21.32$, $p < .001$, *95%CI* = [-0.41; -0.34]). Next we conducted all our analyses only with women who perfectly met all inclusion criteria ($N = 112$ who reported positive LH-tests in their fertile phase and a regular cycle length in both investigated cycles[8]). Results remained virtually identical and can be found in the supplement. In summary, the results remained robust across all checks.

Discussion

In the current study, we sought to clarify whether women experience mate preference shifts for male body masculinity across the ovulatory cycle and, further, investigated potential mediators and moderators of these effects. We conducted a large, pre-registered within-subjects study including assessment of salivary hormones and luteinizing hormone tests. Multilevel intraindividual comparisons across two ovulatory cycles showed significant cycle shifts in women's attraction: When fertile, women's ratings of men's bodies increased for sexual- as well as for long-term attractiveness. Cycle effects were partially mediated by the E/P ratio as well as by lower estradiol and cortisol (sexual attractiveness ratings) and higher progesterone levels (long-term ratings). However, the effects of cortisol and progesterone did

[8] We pre-registered as part of our sampling size determination strategy that we will also report when effect sizes are notably different within the sample of the first $N = 120$. As these 112 women met all inclusion criteria exactly as pre-registered and do not exceed the number of 120, the reported results for these participants could be seen as the pre-registered sample.

not remain significant when excluding the E/P ratio because of possible collinearity problems. Shifts in attraction were only found for women in relationships and were not moderated by self-reported stress, though cycle shifts in sexual attraction disappeared when stress was high. Contrary to previously reported findings, men's masculine body characteristics did not interact with cycle phase to predict sexual attractiveness, indicating no shifts in preferences for specific traits. The same was true for long-term attractiveness.

Cycle effects: preference vs. motivational priority shifts

Our results support the existence of a human female estrus, because we found differences in women's attraction to men's bodies between the fertile and the luteal phase of the ovulatory cycle. Importantly, these results are in contrast to many prior findings. The most widespread perspective in the existing cycle effects literature, derived from the strategic pluralism model, is that women's mate preferences will only shift for men's characteristics that reflect good genes and only when men are evaluated for short-term sexual attractiveness (Gildersleeve et al., 2014a). Contrary to our predictions based on this perspective, but in line with recent literature on ovulatory cycle shifts for masculine faces (Harris, 2011; 2013; Jones et al., in press a; Munoz-Reyes et al., 2014; Peters et al., 2009; Scott et al., 2014) and morphed bodies (Marcinkowska et al., 2018), we did not find evidence for preferences shifts for masculine bodies that could be interpreted as stronger sexual selection for good genes when fertile. Women did not prefer male body masculinity, presumably reflecting good genes, more when they were fertile, compared to their luteal days. In fact, they evaluated exactly the same bodies as more or less attractive, no matter if they rated them in their fertile or their luteal phase. Our findings can rather be interpreted as in line with a motivational priority shift account (Roney & Simmons, 2017). This account entails a shift in motivational priorities towards mating behavior in the fertile phase of the ovulatory cycle, when conception provides a fitness benefit that outweighs the costs of sex, resulting in increased sexual motivation. A fertile phase increase in sexual motivation has repeatedly been found in sexual desire research (e.g., Arslan et al., 2017; Bullivant et al., 2004; Gangestad et al., 2002; 2005; Natale, Albertazzi, & Cangini, 2010; Roney & Simmons, 2013): When fertile, women more frequently initiate sexual behavior, and experience stronger sexual desire and more sexual fantasies. This increase in sexual motivation could probably explain the general increase in attractiveness ratings of masculine bodies in the fertile phase of the ovulatory cycle. However, we have not tested sexual desire in our study. To ascertain that an increase in sexual desire or, more specifically, motivational priority shifts explain our effects, further research should directly test sexual desire as a mediator of cycle shifts in women's attraction.

Relationship status and stress as moderators

In the current study, increasing attractiveness ratings in the fertile phase were significant in the full sample, but further analyses indicated that they held only for women in relationships, not for singles. This effect is also in line with prior research on sexual desire: In a diary study, Roney & Simmons (2016) recently found that only women in relationships, but not singles, experience higher sexual desire in their fertile phase. Similarly, in a small between-subjects study, Havlíček and colleagues (2005) found that only fertile women in relationships rated the smell of dominant men as being particularly sexy, whereas single women did not. The findings of this study were interpreted as indication for a mixed mating strategy in line with the strategic pluralism model (i.e., women preferring men with characteristics of good genes for short-term extra-pair relationships, while seeking men willing to invest in their offspring for long-term relationships). However, since we did neither find differences between sexual- and long-term preferences nor increased attraction to masculinity cues that have been argued to reflect good genes, we suggest a motivational priority shifts as a more parsimonious explanation. If motivational priority shifts occur when fitness benefits of conception outweighs the costs of sex, this might particularly be the case for women in relationships. Single women have more often changing partnerships and might therefore expect higher risks of sexual behavior like infection or injury that are possibly not outbalanced by the benefits of conception in the fertile phase. Furthermore, for women in relationships, a partner who potentially cares for their offspring is available, in contrast to single women, for whom it might be too costly to risk that the offspring's father might not show any paternal effort at all. However, to learn more about the cost/benefit ratio of sex related to relationship status, further research should focus on differences between partnered and single women regarding motivational priority shifts.

Another possible moderator of ovulatory cycle shifts in women's mate preferences in recent research was self-reported stress. Prior studies indicated that stress suppresses an increase in women's masculinity preferences (Ditzen et al., 2017, but see Jones et al., in press a) and decreases estradiol levels (Roney & Simmons, 2015). Nevertheless, we did not find a moderator effect of self-reported stress on cycle shifts in mate attraction, even though cycle shifts in sexual attraction to male bodies disappeared when stress accounted for. However, self-reported stress values are subjective and might not always reflect the physiological stress level. For a clarification of the relationship between stress, cycle shifts and mate preferences, more research is needed.

Hormonal changes as mediating mechanisms

Previous research has found that estradiol positively and progesterone negatively predicts fluctuations in sexual desire (Roney & Simmons, 2013; 2016). Other cycle studies found that women's estradiol level is a predictor of preferences for masculine voices (Pisanski et al., 2014), and higher estimated estradiol levels increased attraction for dominance in long-term mates (Lukaszewski & Roney, 2009). Our results do not entirely support these findings. The increase in sexual- as well as long-term attractiveness ratings for men's bodies were partially mediated by the E/P ratio, validating that the found effect is due to women's fertility status. The effects of cortisol (sexual attractiveness) and progesterone (long-term attractiveness) were not robust in further analyses. Measured salivary estradiol levels were a predictor for sexual attraction only, but in the opposite direction as expected: ratings were higher when estradiol levels were lower. This effect was independent of the effect of the E/P ratio, which is more directly associated with fertility, and might be due to the fact that there is a second, somewhat smaller estradiol peak in the luteal phase (Goodman, 2009) which overlaps with the timing of many luteal phase sessions. However, these results, especially the counter intuitive effect of estradiol, should be replicated before being interpreted further. Furthermore, hormone levels should ideally be measured daily to see if testing sessions in the luteal phase really overlap with the secondary estradiol peak.

Methodological considerations and future research

Many previous studies have reported shifts across the cycle in preferences for masculine cues and other presumed indicators of good genes. Our results on body preferences clearly diverge in this regard, which raises the question of why this might be. One possibility is that we were the first to use natural bodies as stimuli, yielding a higher ecological validity than artificially drawn or morphed stimuli. So far, other published ovulatory cycle effects for body masculinity cues may be contingent on the use of computer-generated bodies, morphed to an artificial, potentially supranatural level of masculinity. We also deviated from earlier studies by not using 2D images or drawings, but rotating 3D models. These models capture natural variation in morphology, the focus of our study, and display it more fully than 2D images or drawings can (compare Marlowe, Apicella, & Reed, 2005). However, since the 3D models were devoid of texture (incl. body hair) and standardized for color, they might also have looked less natural. Therefore our results might have been different if subjects had rated actual photos of bodies rather than 3D representations. Future studies should investigate if our results replicate with different stimulus materials.

Besides the nature of stimuli, there are also other considerable differences between our and prior studies, especially in how to determine women’s fertile days. A substantial fraction of published studies used various calendar-based counting methods (forward or backward counting, or combinations thereof) to estimate the day of ovulation. In addition, some studies used broader (8-9 days in length), others more narrow (6-7 days) fertile windows, or calculated fertility continuously based on different fertility estimates. Many did not use LH tests to validate fertility, although these tests can be seen as the gold standard (Gangestad et al., 2016). Our study did not only use LH tests for validating women's fertile phase, but additionally followed up on all participants to verify their date of the next menstrual onset to be able to backward count to their fertile days. These methods correspond to the state of the art to pinpoint ovulation. Another reason might be that there is huge variation in previous studies in sample sizes and within- vs. between-subjects designs. Many studies only investigated 25 to 50 participants (e.g. Feinberg et al., 2006; Peters et al., 2009), or used between-subject designs (e.g. Havlíček et al., 2005; Little et al., 2007; Pawlowski & Jasienka, 2005). Between-subject ovulatory cycle studies require very large sample sizes to achieve acceptable levels of statistical power (Gangestad et al., 2016), hence within-subject designs should be the designs of choice. The cycle shifts that we found had very small effect sizes. Previous studies worked with relatively small sample sizes. Therefore, they would not have been able to show such small effects. Hence, previously reported effects might have been false positives or due to publication bias. Nevertheless, some of the published studies found evidence for preference shifts in line with the good genes ovulatory shift hypothesis (e.g., Gangestad et al., 2007; Little et al., 2007). Since we had a rather large sample size, used a large number of stimuli and tested all participants four times across two ovulatory cycles, our study had comparatively large power to detect shifts in preferences for masculinity cues. Additionally, in a recent study Marcinkowska and colleagues (2018) also could not replicate cycle shifts in women's preferences for masculinized bodies. However, finding null results running more powerful tests with better methods is not unique to the mate preference literature, but also to other important parts of evolutionary sciences and beyond. For example, Jones and colleagues (in press c) found no evidence that disgust sensitivity tracked changes in hormone levels, contradicting the Compensatory Prophylaxis Hypothesis of pathogen disgust, underlining the importance of high powered study designs. Still, single studies cannot resolve the diverse range of findings in the literature, and more highly powered replication studies will be necessary. Future research should reduce methodological flexibility by agreeing on design and analytic standards and base studies on large sample sizes in order to find out under which circumstances cycle shifts in female mate preferences as well as other previously reported popular effects can be found, and for which characteristics they are robust.

Conclusions

In sum, our findings show that cycle shifts in women’s attraction to male bodies exist, but they do not seem to alter preferences for body characteristics at all, leaving no room for cycle shifts in mate preferences for masculine characteristics or any other assumed indicators of good genes. They are rather in line with a motivational priority shift towards mating effort for women in their fertile phase, resulting in a more favorable evaluation of all male bodies (on average) in terms of sexual- and long-term attractiveness. These shifts appear to be exclusive for women in romantic relationships. Our results contradict some prominent previous findings and indicate that future research is indispensable for clarifying under which conditions cycle shifts can be found and for investigating which findings of previous ovulatory cycle research (e.g., shifts for voices or social dominant behavior; cues to fertility) are robust. Therefore, more and preferably pre-registered studies with a high statistical power and good methodological standards are necessary for finding out the exact relationship between women’s ovulatory cycles, steroid hormones, and their mate preferences.

Acknowledgments

This research was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 254142454 / GRK 2070. We thank Ben Jones and an anonymous reviewer for valuable comments and insightful feedback on an earlier version of this article. Furthermore, we thank Ruben C. Arslan for valuable statistical advice, Christian Treffenstädt for assistance in the programming process, Kelly Gildersleeve for kindly providing a blueprint of an Excel sheet to calculate fertile windows, Alex Stern for helpful comments on prior versions of this manuscript and our research assistants Laura Botzet, Silvia Bradatsch, Paulina Lauer and Laura Specker-Mattißen, without whom this large data collection would not have been possible.

Open practices statement

The study reported in this article was preregistered. The data and instruction material has been made available at the Open Science Framework. We did not post, however, the stimuli videos to protect the privacy of our male participants.

Appendix A. Supplementary data

Supplementary information are available at https://osf.io/n4hj6/

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Appendix B.

Manuscript 2

Jünger, J., Gerlach, T. M., & Penke, L. (2018). *No evidence for ovulatory cycle shifts in women's preferences for men's behaviors in a pre-registered study*. Manuscript in preparation for resubmission. Preprint retrieved from psyarxiv.com/7g3xc. DOI: 10.17605/OSF.IO/7G3XC

Supplementary material and open data are available at https://osf.io/8ntuc/

No evidence for ovulatory cycle shifts in women's preferences for men´s behaviors in a pre-registered study

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Abstract

The existence of ovulatory cycle shifts in women's mate preferences has been discussed controversially. There is evidence that naturally cycling women in their fertile phase, compared to their luteal phase, evaluate specific behavioral cues in men as more attractive for short-term relationships. However, recent research has cast doubt on these findings. We addressed this debate in a large, pre-registered within-subject study including salivary hormone measures and luteinizing hormone tests. One-hundred-fifty-seven female participants rated natural videos of 70 men in flirtatious dyadic interactions on sexual and long-term attractiveness. Multilevel comparisons across two ovulatory cycles revealed significant cycle shifts: When fertile, women's ratings of men's sexual and long-term attractiveness increased. Contrary to previous findings, behavioral cues as displayed in men's flirting behavior did not interact with cycle phase to predict these shifts. Effects were only found for partnered women, not for singles. Hormonal mechanisms and implications for estrus theories are discussed.

Keywords: ovulatory cycle, mate preferences, steroid hormones, fertility, attractiveness, flirting behavior

Introduction

Scientific interest in whether women experience systematic psychological changes across their ovulatory cycle has increased in recent years. A substantial amount of research indicates that women's sexual interests change across the ovulatory cycle. Roney and Simmons (2013; 2016) showed that women's level of sexual desire is higher during their fertile phase, mediated by higher estradiol and lower progesterone levels. These changes in sexual desire could be replicated in other studies (e.g. Arslan, Schilling, Gerlach, & Penke, 2017; Grebe, Thompson, & Gangestad, 2016; Shirazi et al., 2018). While cycle shifts in sexual desire appear robust, there is ongoing discussion whether there are changes in mate preferences as well. According to the good genes sexual selection account (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007), women should seek sexual partners with high heritable fitness, presumably indicated by for example masculine traits, symmetry or dominant behavior, to acquire good genes for their offspring. Mating with these men can be costly though, because they may be less willing to provide parental effort (Gangestad & Simpson, 2000). As such, they might not be a good choice for long-term relationships. To solve this dilemma, women's mate preferences were hypothesized to differ according to the mating context (Pillsworth & Haselton, 2006): When fertile, women should prefer men with characteristics indicative of good genes for sexual relationships. These preferences should be absent in the luteal phase (i.e., between ovulation and menstrual onset) and when evaluating men for long-term relationships (Gangestad, Thornhill, & Garver-Apgar, 2005).

Evidence for this good genes ovulatory shift hypothesis (GGOSH) is mixed. Previous research has documented cycle shifts in women's mate preferences (e.g. Feinberg et al., 2006; Gangestad et al., 2007; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Gangestad & Thornhill, 1998; Havlíček, Roberts, & Flegr, 2005; Puts, 2005) for several physical (male faces, bodies, voices, odor) and behavioral traits (e.g., dominance, social presence). However, changes in preferences for masculine faces and bodies did not replicate in more recent research (e.g. Harris, 2013; Jones et al., in press; Jünger, Kordsmeyer, Gerlach, & Penke, 2018; Marcinkowska, Galbarczyk, & Jasienska, 2018; Muñoz-Reyes et al., 2014; Peters, Simmons, & Rhodes, 2009). Moreover, two meta-analyses have come to strikingly diverging conclusions on whether cycle effects exist or not (Gildersleeve, Haselton, & Fales, 2014; Wood, Kressel, Joshi, & Louie, 2014). In sum, to clarify the scientific discourse about the existence of ovulatory cycle shifts, there is strong need for adequately powered replications.

In the current study, we set out to directly probe the GGOSH for men's behaviors. In particular, we aimed to clarify a) whether there are preference shifts for men's behaviors across the ovulatory cycle, b) which hormonal mechanisms might potentially mediate these effects and c) which moderators affect them.

Overview of the current study and hypotheses

Investigating ovulatory shifts in preferences for men´s flirting behavior

Several studies show that women's preferences for men displaying behavioral dominance, confidence, and social presence change across the ovulatory cycle (Gangestad et al., 2004; 2007; Lukaszewski & Roney, 2009). These behaviors usually include intrasexual competition between two men (Gangestad et al., 2004), but in most mating situations nowadays, women are confronted with one men, not with two or more competing. Therefore, we decided to investigate cycle shifts in preferences for men´s flirting behavior and dominance-related cues found in such behavior, like self-displays or speaking time.

Prior research has already reported changes in women's flirting behavior and behavioral engagement towards men with purported markers of genetic fitness (Cantú et al., 2014; Flowe, Swords, & Rockey, 2012). Moreover, women seem to show preferences for flirtatious facial movement in the fertile phase of the ovulatory cycle (Morrison, Clark, Gralewski, Campbell, & Penton-Voak, 2010), but it remains unclear if they also shift their preferences regarding men's behavior. Following previous findings on ovulatory cycle shifts in mate preferences, we hypothesize that fertile women, as compared to when in their luteal phase, evaluate men's flirting behavior as more attractive for sexual relationships (Hypothesis 1). Building on prior studies, we derived cues for which cycle shifts, if existent, should occur (Gangestad et al., 2004; 2007; Cantú et al., 2014). When fertile, women should be more sexually attracted to men who show more overt flirting behavior, more self-displays, more direct gazes towards the women they were talking to, and more behavior that is consensually perceived as attractive (*behavioral attractiveness*; Hypothesis 2a). When evaluating long-term attractiveness, preference shifts should be absent or only weakly present (Hypothesis 3). In an exploratory manner, we will also investigate two nonverbal flirting cues: men's a) amount of speaking time and b) amount of smiles in the presented video. We predict our findings to be robust when controlling for men's age, physical attractiveness and voice attractiveness. We also state the alternative hypothesis that women will not show cycle shifts in their mate preferences regarding men's behaviors for sexual relationships (Hypothesis 2b).

Hormones as mediators, relationship status as a moderator

Women's ovulatory cycle is regulated by shifts in hormone concentrations (Lukaszewski & Roney, 2009). While estradiol rises in women's fertile phase, it decreases during the luteal phase, but with a second smaller peak mid-luteal. Progesterone levels are usually lower in the fertile phase and higher in the luteal phase. Therefore, cycle shifts in mate preferences should be regulated by natural changes in steroid hormone levels: higher estradiol and lower progesterone (Hypothesis 4). Moreover, the estradiol-to-progesterone-ratio is a superior index for fertility (Baird, Weinberg, Wilcox, McConnaughey, & Musey, 1991), with a higher estradiol-to-progesterone-ratio characterizing the fertile phase and a lower ratio characterizing the luteal phase. In addition, recent research suggests to also investigate testosterone (Bobst, Sauter, Foppa, & Lobmaier, 2013; Roney & Simmons, 2013; Welling et al., 2007) and cortisol (e.g. Ditzen, Palm-Fischbacher, Gossweiler, Stucky, & Ehlert, 2017) as possible regulatory hormones. In the current study, these hormones were analyzed in an exploratory manner.

An important variable that might affect the strengths of ovulatory cycle shifts is women's relationship status. According to the dual mating hypothesis, women may receive fitness benefits when forming a relationship with a reliably investing man, while seeking good genes from other men through extra-pair sexual encounters (Pillsworth & Haselton, 2006). Since it remains unclear if singles also pursue different mating strategies across the cycle, we state two alternative hypotheses: Cycle shifts in preferences for short-term mates will be larger for partnered women than for single women (Hypotheses 5a), or, alternatively, relationship status will not affect the strengths of cycle shifts in preferences for short-term mates (Hypotheses 5b).

Overcoming methodological problems: Power and reduced flexibility

In the current study, we directly addressed potentially serious methodological problems from prior studies that might responsibly cause the uncertainty about the existence of cycle shifts in women's mate preferences. All prior studies that investigated cycle shifts for behavioral cues have used inappropriate samples sizes (Gangestad et al., 2016): They either recruited less than 50 participants (e.g. Cantú et al., 2014; Morrison et al., 2010) or used between-subjects instead of higher-powered within-subjects designs (Flowe et al., 2012; Gangestad et al., 2004; 2007; Lukaszewski & Roney, 2009; Morrison et al., 2010). Furthermore, all studies lacked direct assessments of steroid hormones and most of them did not use luteinizing hormone (LH) tests for validating women's fertile phase. They rather estimated hormone levels and cycle phase by different counting methods only (Gangestad et al., 2004; 2007; Lukaszewski & Roney, 2009; Morrison et al., 2010). Finally, in light of the current replication crisis (Open Science Collaboration, 2015), it is also important to note that none of the prior studies was pre-registered or offered open data or material.

Material and Methods

Our hypotheses, the study design, the sampling and the analysis plan have been pre-registered online at the Open Science Framework (https://osf.io/egjwv/?view_only=91eb519f6d684637a47d1333c5f8856a), before any data have been collected or analyzed. This pre-registration also contained further hypotheses that are not part of the present paper. Open data, analysis script and instruction material is also provided. All participants signed a written consent form and the local ethics committee approved the study protocol (no. 144).

Participants and Recruitment

Participants were recruited based on the inclusion criteria of other ovulatory cycle studies and had to fit to the following preregistered criteria: female, between 18 and 30 years old, naturally cycling (no hormonal contraception for at least three months, no expected switch to hormonal contraception during the study, no current pregnancy or breastfeeding, no birth-giving or breast-feeding during the previous three months, not taking hormone-based medication or anti-depressants). Additionally, they had to report that their ovulatory cycles had a regular length between 25 and 35 days during the last 3 months.

In total, we recruited 180 participants, of whom 23 could not be included in the final sample. Seventeen women who only attended the introductory session of the study dropped out before participation (six fulfilled one of the exclusion criteria below, four quit the study without further reasons, four did not respond to emails, three had scheduling problems). Another six dropped out during the study because of only completing the first testing session (four had scheduling problems, two did not respond to emails after the first session). One of the participants reported to be 35 years old. We included her data because she met all other including criteria and had positive LH-tests. Excluding her data did not change the results. One-hundred-fifty-seven heterosexual female participants (aged 18-35, M = 23.3, SD = 3.4) finished all sessions and could therefore be included in further analyses. At the beginning of the study, 75 of these participants reported to be in a relationship, 82 reported to be single. Our within-subject sample size largely exceeded those required to achieve 80% power given anticipated effects of moderate magnitude (Cohen's $d = 0.5$) as suggested per recent guidelines for sample sizes in ovulatory shift research (Gangestad et al., 2016). Upon completion of all sessions (see Procedure below), participants received a payment of 80€ or course credit.

Procedure

All participants took part in five individually scheduled sessions. In the first introductory session, participants received detailed information about the general procedure, duration of the study and compensation. Furthermore, the experimenter explained the ovulation tests and checked the inclusion criteria. To count the days to the next ovulation and to plan the dates of the experimental sessions, cycle length as well as the dates of the last and the next menstrual onset were assessed. Finally, demographic data was collected.

Sessions two to five, the computer-based testing sessions, took place once during the fertile phase and once during the luteal phase for two consecutive cycles per participant. To control for possible effects of diurnal changes in hormone levels, all sessions took place in the second half of the day (mainly between 11.30 am and 6 pm). When arriving at the lab, participants first completed a screening questionnaire, assessing their eligibility and some control variables for the saliva samples (Schultheiss & Stanton, 2009). Saliva samples were collected via passive drool before the participants started the first rating task. Participants also had to complete other rating tasks and anthropometric data was collected between these tasks (as part of a larger study, see pre-registration).

In the first testing session, participants saw a short preview video, presenting facial pictures of all men they were about to rate, for one second each. In preparation of viewing of the video clips that were the actual stimulus material, participants were instructed to evaluate the men's attractiveness as they perceived it “in that moment”, independent of their own current relationship status or general interest in other men, and to rate the attractiveness of the men by focusing only on the behavior as exhibited in the videos.

Participants were then presented with the video clips in a randomized order. After watching each sequence, participants were to rate each individual man separately regarding sexual attractiveness (assessing short-term attraction) and attractiveness for long-term relationships. Ratings were done on eleven-point Likert scales from -5 (*extremely unattractive*) to +5 (*extremely attractive*), including zero as a neutral point. Definitions of sexual attractiveness and attractiveness for a long-term relationship were provided prior to the rating task:

a) *Sexually attractive*: Men that score high would be very attractive for a sexual relationship that can be short-lived and must not contain any other commitment. Men scoring low would be very unattractive for a sexual relationship.
b) *Attractive for a long-term relationship*: Men that score high would be very attractive for a committed relationship with a long-term perspective. Men that score low would be very unattractive as a long-term partner.

After each session, the appointment for the next session was arranged individually based on the participant's ovulatory cycle.

Measures

Ovulatory cycle phase

Women's cycle phase was determined by the reverse cycle day method, based on the estimated day of the next menstrual onset (Gildersleeve, Haselton, Larson, & Pillsworth, 2012) and confirmed by highly sensitive (10 mIU/ml) urine ovulation test strips from purbay®, which measure the luteinizing hormone (LH). These LH-tests had to be done at home at the estimated day of ovulation and the four days prior to that. The study investigated two ovulatory cycles in which each participant reported to the lab twice: Once while being fertile (at the days immediately preceding ovulation, usually reverse cycle day 16-18, with reverse cycle day 16 as the most ideal date) and once when not fertile (during the luteal phase, after ovulation and prior to the next menstrual onset, usually reverse cycle day 4-11, with reverse cycle days 6 to 8 as the most ideal dates). Of all participants who finished every session, 66 participants started with the first session in their luteal phase, 91 started in the fertile phase.

Stimuli and behavioral ratings

Thirty seconds long sequences of videos of men in dyadic interactions, recorded in a study on sociosexuality (Penke & Asendorpf, 2008), were presented. We selected the videos of 70 men that were single at the time of the initial study out of a larger pool of 283 videos in total. For every video, a male participant was seated in a room with an attractive female confederate. They were instructed to get to know each other, while the experimenter left the room (see Penke & Asendorpf, 2008, for details). From each conversation, we took the sequence from 02:00 to 02:30 minutes to avoid the awkwardness of the first moments and ensure that the interaction was in full flow. The participants saw the conversation from a camera recording over the shoulder of the female confederate, so that they saw a frontal view of only the man in each interaction.

To get the behaviors of all men, videos were rated by four independent, trained raters (two women, two men) that were unacquainted with the participants. Ratings were done using 7-point Likert scales for the 30-seconds sequences on the following behavioral dimensions: flirting behavior, self-displays, and behavioral attractiveness. Ratings were collected in two rounds, the first based on recordings from a side perspective, the second based on the frontal recordings that were used as stimuli in the present study. In both rounds, videos were presented with audio. Interrater agreement was high (side perspective: $\alpha = .84$ to .88; frontal perspective: $\alpha = .85$ to .90), thus ratings of all raters and both perspectives were aggregated. In addition, codings of the objective behaviors were done with Noldus Observer by two trained research assistants. Codings from both assistants were averaged. We used the following behaviors: percentage of time the man smiles (*men's smiles*), percentage of time the man speaks (*men's speaking time*) and percentage of total amount of time the man gazed directly at the confederate's face (*men's gazes*). Intraclass correlations were high, ranging from .86 to .99. Additionally, for control analyses, men's facial and vocal attractiveness were also rated on 7-point Likert scales. For facial attractiveness, frontal face pictures with a neutral facial expression were rated by 15 different undergraduate students each. Interrater reliabilites were high, so that ratings were aggregated after z standardization. For vocal attractiveness, voice recordings (counting from 1 to 10) were rated by six trained research assistants and ratings were totalized afterwards. Behaviors varied distinctly between the videos, descriptive values for all can be found in the supplement. More details about the rating and coding procedures can be found in Penke and Asendorpf (2008).

Hormone assessments

For hormone assays, we collected four saliva samples from each participant (one per testing session). Contamination of saliva samples was minimized by asking participants to abstain from eating, drinking (except plain water), smoking, chewing gum or brushing teeth for at least one hour before each session. The samples were stored at -80°C directly after collection until shipment on dry ice to the Kirschbaum Lab at Technical University of Dresden, Germany, where estradiol, progesterone, testosterone and cortisol was assessed via liquid chromatography mass spectrometry (LCMS). In only 22% of the hormone samples estradiol levels could be detected at all by LCMS analysis. Therefore, the samples were reanalyzed using a highly sensitive 17β-estradiol enzyme immunoassay kit (IBL International, Hamburg, Germany). These latter estradiol values were used in subsequent analyses. We centered all hormone values on their subject-specific means and scaled them afterwards so that the majority of the distribution for each hormone varied from -0.5 to 0.5 (as in Jones et al., in press; Jünger et al., 2018). This is a common procedure to isolate effects of within-subject changes in hormones, avoiding the influence of outliers on results and dealing with the non-normal distribution of hormone levels.

Results

Preliminary Analyses

First we checked how many of the participants' ovulatory cycles had positive LH tests (showing a LH surge) in the calculated fertile phase to detect non-ovulatory cycles. Twelve participants reported negative LH test results for both investigated cycles, nine reported negative LH tests results for one cycle. In total, the LH tests in 33 of all 314 cycles (10.5%) were negative. Next, we counted how many cycles were reported as being irregular, that is, the days of the testing sessions did deviate from the prior defined phase of appropriate testing days by more than three days (see section "ovulatory cycle phase"). Eight women reported irregular cycles in both investigated cycles, 32 reported one cycle being irregular, resulting in 48 out of 314 (15.3%) cycles being irregular (despite all participants reporting having regular ovulatory cycles in the introductory session prior to the testing sessions). Participants with irregular cycles or negative LH tests were still included in the main analyses, but excluded in robustness checks.

Main analyses: Cycle shifts in women's attraction and mate preferences

We first tested for possible ovulatory cycle shifts in women's attractiveness ratings for men's behavior in general (Hypotheses 1 and 3). For the multilevel analyses with attractiveness rating as dependent variable (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness), female raters and male stimuli were treated as random effects. Women's cycle phase (0 = luteal phase, 1 = fertile phase) was treated as a fixed effect. Both models showed a significant cycle shift in women's attraction: When fertile, ratings for sexual attractiveness were higher than in the luteal phase of the ovulatory cycle ($\gamma = 0.08$, $SE = 0.02$, $t = 3.87$, $p < .001$, 95%CI = [0.04; 0.11]), supporting Hypothesis 1. Similar results were found for the long-term attractiveness ratings ($\gamma = 0.07$, $SE = 0.02$, $t = 3.70$, $p < .001$, 95%CI =

[0.03; 0.11]), contrary to Hypothesis 3. Figure 1 shows how women's attraction changes as a function of cycle phase. When women were fertile, the attractiveness ratings of men's flirting behavior increased compared to the ratings in the luteal phase.

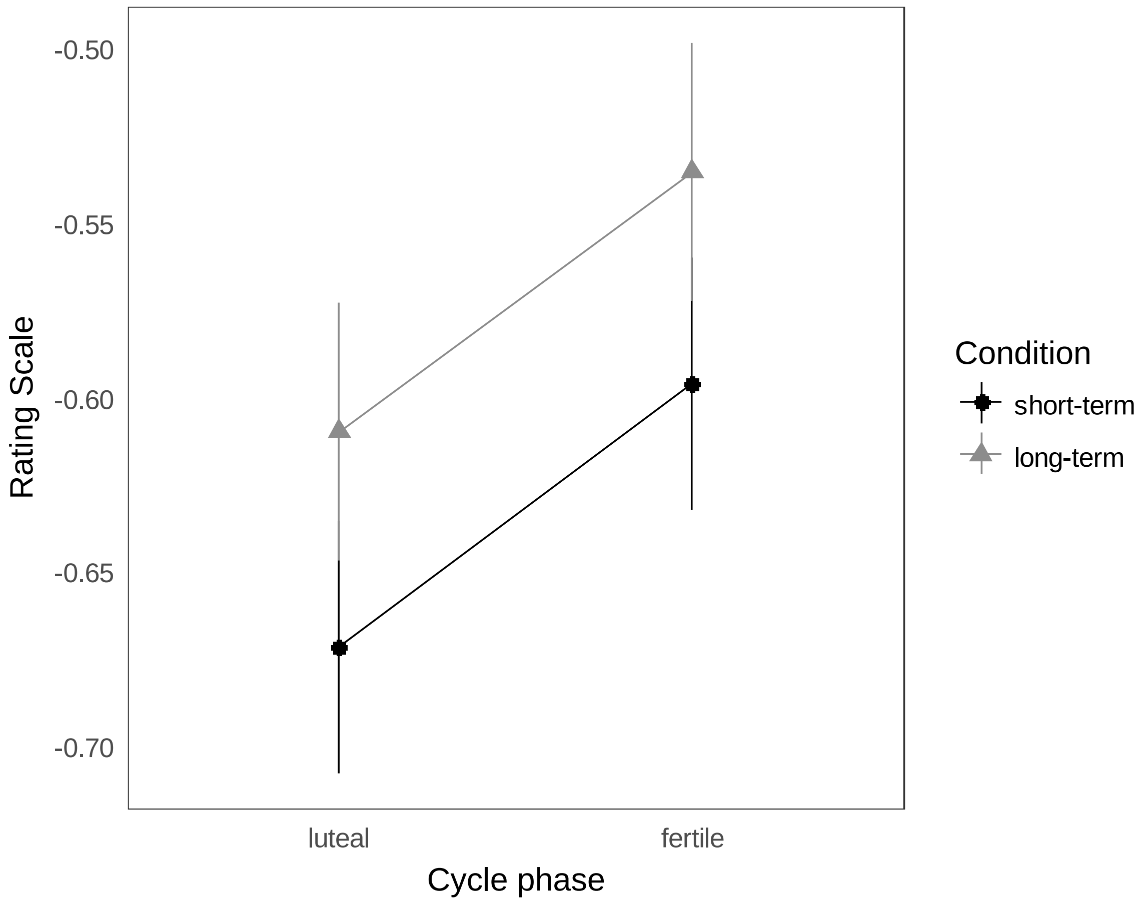

Figure 1. Averaged attractiveness ratings for short-term sexual and long-term relationships in function of women's cycle phase. Rating scale ranges from -5 to +5, the Y-axis is truncated. Error bars represent 95% confidence intervals.

To analyze whether women's mate preferences for specific behaviors changed across the cycle (Hypotheses 2a, 2b and 3), we calculated two further multilevel models (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness as dependent variable). In both models, women's cycle phase and the behaviors flirting behavior, self-display behavior, behavioral attractiveness, direct gazes towards the female interaction partner, men's speaking time, and men's smiles were treated as fixed effects. In addition, men's vocal attractiveness, facial attractiveness, and age were entered as covariates and also treated as fixed effects. Female participants as well as male stimuli were treated as random effects. Results showed that none of the behaviors interacted with cycle phase, indicating that women's mate preferences for specific cues in men's behavior did not shift across the ovulatory cycle, contradicting Hypothesis 2a, but supporting alternative Hypothesis 2b. However, there were significant main effects for cycle phase, flirting behavior, behavioral attractiveness facial attractiveness and men's age on sexual attractiveness ratings (Table 1). The effects were comparable for long-term attractiveness ratings, except facial attractiveness and men's age did not reach levels of significance (Table 2). These results again support Hypothesis 1 and contradict Hypothesis 3. In sum, women rated men's behavior as more attractive when they were fertile, when men showed more flirting behavior, behaved more attractive, had more attractive faces and were younger. This was true for sexual as well as for long-term attraction, in spite the main effects of facial attractiveness and age.

Table 1

Results of multilevel regression analyses of sexual attractiveness ratings.

	γ	*SE*	*t*	*p*	95% CI
Women's cycle phase	0.08	0.02	3.87	<.001	[0.04, 0.11]
Men's flirting behavior	0.57	0.17	3.31	.002	[0.25, 0.89]
Men's self-display behavior	0.18	0.15	1.21	.231	[-0.09, 0.45]
Men's behavioral attractiveness	0.46	0.15	3.01	.004	[0.18, 0.74]
Men's gazes	0.17	0.12	1.42	.160	[-0.05, 0.40]
Men's speaking time	-0.02	0.15	-0.15	.885	[-0.29, 0.25]
Men's smiles	-0.12	0.14	-0.89	.379	[-0.37, 0.13]
Men's vocal attractiveness	0.15	0.11	1.36	.179	[-0.05; 0.35]
Men's facial attractiveness	0.31	0.13	2.30	.025	[0.06; 0.55]
Men's age	-0.23	0.11	-2.03	.047	[-0.43; -0.02]
Cycle phase x Men's flirting behavior	0.01	0.03	0.45	.651	[-0.05, 0.07]
Cycle phase x Men's self-display behavior	-0.02	0.03	-0.71	.480	[-0.07, 0.03]
Cycle phase x Men's behavioral attractiveness	0.00	0.03	0.18	.854	[-0.05, 0.06]
Cycle phase x Men's gazes	0.01	0.02	0.34	.734	[-0.04, 0.05]
Cycle phase x Men's speaking time	-0.02	0.03	-0.61	.542	[-0.07, 0.04]
Cycle phase x Men's smiles	-0.01	0.03	-0.54	.591	[-0.06, 0.04]

Note. Women's cycle phase, men's behaviors and their interactions as predictors of sexual attractiveness ratings. All variables had 43,960 observations (157 participants x 4 test sessions x 70 stimuli). Cycle phase was dummy-coded (0 = luteal, 1 = fertile). All values were z-standardized.

Table 2

Results of multilevel regression analyses of long-term attractiveness ratings.

	γ	*SE*	*t*	*p*	95% CI
Women's cycle phase	0.07	0.02	3.70	<.001	[0.03, 0.11]
Men's flirting behavior	0.63	0.17	3.63	<.001	[0.31, 0.95]
Men's self-display behavior	0.11	0.15	0.74	.465	[-0.17, 0.39]
Men's behavioral attractiveness	0.43	0.15	2.82	.006	[0.15, 0.72]
Men's gazes	0.21	0.12	1.75	.085	[-0.01, 0.44]
Men's speaking time	-0.05	0.15	-0.32	.750	[-0.32, 0.23]
Men's smiles	-0.13	0.14	-0.98	.331	[-0.39, 0.12]
Men's vocal attractiveness	0.12	0.11	1.12	.268	[-0.08; 0.32]
Men's facial attractiveness	0.22	0.13	1.62	.110	[-0.03; 0.47]
Men's age	-0.20	0.11	-1.76	.083	[-0.41; 0.01]
Cycle phase x Men's flirting behavior	0.02	0.03	0.63	.529	[-0.04, 0.08]
Cycle phase x Men's self-display behavior	-0.02	0.03	-0.66	.511	[-0.07, 0.04]
Cycle phase x Men's behavioral attractiveness	-0.01	0.03	-0.25	.807	[-0.06, 0.05]
Cycle phase x Men's gazes	0.01	0.02	0.26	.795	[-0.04, 0.05]
Cycle phase x Men's speaking time	-0.03	0.03	-0.92	.358	[-0.08, 0.03]
Cycle phase x Men's smiles	-0.01	0.03	-0.33	.744	[-0.06, 0.04]

Note. Women's cycle phase, men's behaviors and their interactions as predictors for long-term attractiveness ratings. All variables had 43,960 observations (157 participants x 4 test sessions x 70 stimuli). Cycle phase was dummy-coded (0 = luteal, 1 = fertile). All values were z-standardized.

Our decision to include all behaviors as fixed effects in one single model might have caused collinearity problems (correlations of the behaviors can be found in the supplement). Therefore, we additionally calculated separate models for all behaviors for sexual attractiveness ratings (see open script). In each model, the significant attraction shift of cycle phase stayed significant and none of the behaviors interacted with cycle shifts, indicating that mate preferences do not shift across the cycle. Again, we found some main effects for the behaviors: ratings were higher when flirting behavior, self-display behavior and behavioral attractiveness were high. There were no significant main effects for gazes, smiles or speaking time. We also calculated separate models including behaviors for only the pre-registered or the exploratory variables. Overall, results did not change; details can be found in the supplement.

Next, to better understand the nature of the observed the cycle effect women's attraction, we calculated Spearman rank correlations between sexual attractiveness ratings in the fertile and those in the luteal phase. Ranks of the rated videos were almost perfectly correlated and this was true for sexual ($r = .996$, $p < .001$) as well as for long-term attractiveness ($r = .994$, $p < .001$), indicating that women rated the same men as more or less attractive across the different cycle phases. These close-to-perfect rank correlations do not leave room for cycle phase to interact with men´s behaviors to predict attractiveness ratings. Further, these results substantiate there is a general increase in attractiveness perceptions of all kinds of men, not specific men, experienced by our participants when fertile.

Hormonal mechanism potentially underlying cycle shifts

To investigate possible mediating effects of steroid hormones underlying cycle shifts in women's attraction (Hypothesis 4), we entered estradiol, progesterone, estradiol-to-progesterone ratio, testosterone, and cortisol as fixed effects to our multilevel model, female participants and male stimuli as random effects, and women's cycle phase as another fixed effect. Results showed that cycle shifts for sexual attractiveness ratings were partially mediated by women's estradiol levels: ratings were higher when women's estradiol levels were higher (see Table 3), only partially supporting Hypothesis 4. For long-term attractiveness ratings, we found a partial mediation of cycle shifts by the estradiol-to-progesterone-ratio: ratings were higher when the E-P ratio was lower. There were no significant effects for progesterone, testosterone, or cortisol. For both attractiveness ratings, the effect of cycle phase stayed significant, again corroborating that ratings increased in women's fertile phase compared to ratings during the luteal phase.

Table 3

Multilevel regression analyses testing for mediator effects of steroid hormones on the effect of cycle phase on attractiveness ratings.

	γ	*SE*	*t*	*p*	95% CI
Sexual					
Cycle phase	0.10	0.03	3.64	.001	[0.04; 0.15]
Estradiol	0.01	0.00	2.58	.010	[0.00; 0.02]
Progesterone	-0.00	0.00	-0.09	.925	[-0.00; 0.00]
E/P	-0.01	0.01	-1.47	.143	[-0.03; 0.00]
Testosterone	0.00	0.00	0.55	.584	[-0.00; 0.00]
Cortisol	-0.00	0.00	-0.08	.935	[-0.01; 0.00]
Long-term					
Cycle phase	0.08	0.03	2.98	.003	[0.03; 0.14]
Estradiol	0.01	0.00	1.89	.060	[-0.00; 0.02]
Progesterone	0.00	0.00	0.71	.476	[-0.00; 0.00]
E/P	-0.02	0.01	-2.49	.013	[-0.04; -0.00]
Testosterone	0.00	0.00	0.93	.351	[-0.00; 0.00]
Cortisol	-0.00	0.00	-0.93	.351	[-0.01; 0.00]

Note. All variables had 37,380 observations (157 participants x 4 test sessions x 70 stimuli – missing values). Cycle phase was dummy-coded (0 = luteal, 1 = fertile). E/P = estradiol-to-progesterone-ratio. All hormone values were centered to their subject-specific means and then scaled.

Our decision to include all hormone levels as fixed effects in one single model might have caused collinearity problems. Therefore, we additionally calculated separate models (Model 1 for estradiol and progesterone, Model 2 for the estradiol-to-progesterone-ratio, Model 3 for testosterone and cortisol) for sexual as well as long-term attractiveness ratings. Again, overall results did not change, including all hormone levels in the same model versus calculating separate models did not affect the results.

The role of women's relationship status for ovulatory cycle shifts

In order to analyze whether women's relationship status might moderate ovulatory cycle shifts (Hypothesis 5), we categorized all women as being in a relationship who reported to be in an open relationship, in a committed relationship, engaged, or married. However, results did not change when categorizing women who reported to be in an open relationship as singles instead. Relationship status changed for 13 women across the study; these cases were categorized according to their relationship status on the particular testing day. Two multilevel models (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness as outcome), with women's cycle phase and their relationship status as fixed effects and female participants and male stimuli as random effects showed significant interaction effects between cycle phase and relationship status (Table 4). These results indicate that only women in relationships showed cycle shifts in their attraction for behaviors. The main effect of cycle phase was no longer significant for sexual or long-term attractiveness ratings. There was a main effect for relationship status in long-term attractiveness ratings, showing that single women rated men's behavior in the videos as more attractive for long-term relationships compared to the partnered women. This effect was not significant for sexual attractiveness ratings. Taken together, these results support Hypothesis 5a, but not alternative Hypothesis 5b.

Table 4

Multilevel regression analyses of attractiveness ratings as a function of cycle phase and women's relationship status.

	γ	*SE*	*t*	*p*	95% CI
Sexual					
Cycle phase	0.02	0.03	0.76	.449	[-0.03; 0.07]
Relationship status	-0.06	0.07	-0.79	.431	[-0.20; 0.08]
Cycle phase x Relationship status	0.12	0.04	2.93	.003	[0.04; 0.19]
Long-term					
Cycle phase	0.03	0.03	1.19	.234	[-0.02; 0.09]
Relationship status	-0.21	0.07	-2.88	.004	[-0.36; -0.07]
Cycle phase x Relationship status	0.09	0.04	2.23	.026	[0.01; 0.17]

Note. All variables had 43,960 observations (157 participants x 4 test sessions x 70 stimuli). Cycle phase (0 = luteal, 1 = fertile) and relationship status (0 = single, 1 = in relationship) were dummy-coded.

Robustness checks

We conducted further analyses to probe the robustness of our effects. To rule out that our results might have been caused by order effects of testing sessions, particularly participating in the first session when fertile (Suschinsky, Bossio, & Chivers, 2014), we controlled for type of first phase in our analyses. Starting fertile vs. luteal did affect the attractiveness ratings (sexual: $\gamma = 0.52$, *SE* = 0.14, $t = -3.68$, $p = <.001$, 95%CI = [0.24; 0.81]; long-term: $\gamma = 0.39$, *SE* = 0.15, $t = 2.56$, $p = .011$, 95%CI = [0.09; 0.69]), indicating that ratings were higher when participants started in the fertile phase. However, for both sexual and long-term attractiveness ratings the effect of cycle phase remained stable (sexual: γ = 0.08, *SE* = 0.02, *t* = 3.87, *p* < .001, 95%CI = [0.04; 0.11]; long-term: γ = 0.07, *SE* = 0.02, *t* = 3.70, *p* < .001, 95%CI = [0.04; 0.11]). Next, we added a variable for values of the first vs. the second tested ovulatory cycle as fixed effect to our basic model, with cycle phase as another fixed effect, and female raters and male stimuli as random slopes, to see if there were differences in ratings. Ratings were significantly higher in the second cycle across all participants (sexual: γ = 0.20, *SE* = 0.02, *t* = -18.62, *p* < .001, 95%CI = [0.17; 0.24]; long-term: γ = 0.09, *SE* = 0.02, *t* = 4.50, *p* < .001, 95%CI = [0.05; 0.13]). Nevertheless, for both sexual and long-term attraction the effects of cycle phase again remained stable (sexual: γ = 0.08, *SE* = 0.02, *t* = 3.88, *p* < .001, 95%CI = [0.04; 0.11]; long-term: γ = 0.07, *SE* = 0.02, *t* = 3.70, *p* < .001, 95%CI = [0.03; 0.11]). We then repeated our analyses with only those women who perfectly met all inclusion criteria, i.e., *n* = 112 who reported positive LH-tests in their fertile phase and a regular cycle length in both investigated cycles. As part of our sample size determination strategy we pre-registered that we will also report when effect sizes are notably different within the sample of the first *n* = 120. As these 112 women met all inclusion criteria exactly as pre-registered and do not exceed the number of 120, the reported results for these participants can be seen as the pre-registered sample. Results remained virtually identical and can be found in the supplement. In summary, the results remained robust across all checks.

Discussion

Our study makes three important contributions to the ongoing ovulatory cycle shift debate: First, when fertile, women evaluate men’s behavior as more attractive for sexual- as well as for long-term relationships. This effect is only present for women in relationships. Second, shifts in sexual attraction are partially mediated by higher estradiol levels, shifts in long-term attraction partially mediated by a lower estradiol-to-progesterone-ratio. Third, cycle shifts in preferences for specific behaviors could not be found here.

These findings run contrary to effects reported previously and interpreted as evidence for the GGOSH. Women's attraction to men, but not their mate preferences, shifts across the ovulatory cycle, regardless of potential indicators of good genes. At first glance, the result that shifts only occur for partnered women might seem to fit to a dual mating strategy (Pillsworth & Haselton, 2006): Partnered women could search for fitness benefits from men with good genes through extra-pair sexual encounters when fertile, especially when their primary partner lacks attractiveness. However, contrary to this account, we did not find evidence for preference shifts for specific behaviors that could be interpreted as stronger sexual selection for good genes when fertile. Additionally, attraction also shifted for long-term ratings and a recent study found no moderation of partner attractiveness for extra-pair desire (Arslan et al., 2017). These findings clearly speak against the basic assumptions of the dual mating strategy and the GGOSH.

Nevertheless, it could be adaptive that increased fertile phase attraction to men only occurs for partnered women. Paternal investment for their offspring is only available for partnered women, not for singles. This expectation of resource security might be necessary to trigger general sexual desire in fertile women, which might be transferable to target men other than the primary partner. Of course, single women experience sexual desire as well, but conceiving may yield higher fitness benefits for women when parental investment is available, therefore only sexual desire in partnered women might be adaptively designed to lead to increased fertile phase attraction to men. In line with this interpretation, neuronal systems for pair bonding and sexual desire appear to be particularly interdependent and closely connected in women (Diamond, 2003).

The motivational priority shifts theory (Roney & Simmons, 2017) might also explain our results. This theory proposes a shift in motivational priorities from feeding and foraging towards sexual behavior in the fertile phase of the cycle, because then conception provides a fitness benefit that outweighs the costs of sex. Also in line with this account, the cost-benefit ratio of sexual behavior in the fertile should be particularly high for partnered women, again because of available paternal investment. A resulting increase in sexual motivation in the fertile phase is probably linked to the general increase in women's attraction to men's behavior. However, to probe the validity of the motivational priority shifts account, future research should try to directly pit this account against other competing theories from the literature (e.g. cycle shifts as vestigial by products of hormonal changes, Thornhill & Gangestad, 2015, or the "spandrels hypothesis": cycle shifts as a by-product of between-women hormonal differences, Havlíček, Cobey, Barrett, Klapilová, & Roberts, 2015). Additionally, future studies should closer investigate differences between singles and partnered women in sexual desire and motivation to better understand why fertile phase attraction shifts exclusively occur for partnered women.

The current study reported mediator effects of hormone levels. The finding that higher estradiol levels lead to increased sexual attraction in the fertile phase is consistent with prior evidence suggesting that estradiol predicts extra-pair sexual motivation (Grebe et al., 2016; Roney & Simmons, 2013). However, the negative association of long-term attraction and the estradiol-to-progesterone-ratio is rather counter-intuitive and does not fit to any known theoretical account. Notably, there is a chance that this finding is false positive (p = .013). We suggest that this finding should be replicated before further interpretation.

In conclusion, in the largest study conducted so far investigating possible cycle shifts in women's mate preferences for men's behaviors, we showed that partnered women's attraction to men increased in the fertile phase, but mate preferences did not shift. As such, our findings are inconsistent with the GGOSH, yet may support a motivational priority account of ovulatory cycle effects.

Author contributions

J. Jünger and L. Penke developed the study concept and contributed to the study design. Testing and data collection were performed by J. Jünger, who also performed data analysis and interpretation under the supervision of L. Penke. J. Jünger drafted the manuscript and T. M. Gerlach and L. Penke provided critical revisions. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The authors declare that they have no conflicts of interests with respect to their authorship or the publication of this article.

Acknowledgments

This research was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 254142454 / GRK 2070. We thank Ruben C. Arslan for valuable statistical advice, Christian Treffenstädt for assistance in the programming process, Kelly Gildersleeve for kindly providing a blueprint of an Excel sheet to calculate fertile windows, Alex Stern for comments on prior versions of this manuscript and our research assistants Laura Botzet, Silvia Bradatsch, Paulina Lauer and Laura Specker-Mattißen, without whom this large data collection would not have been possible.

Open practices statement

The study reported in this article was preregistered. The preregistration, data, analysis script and instruction material has been made available at the Open Science Framework (https://osf.io/egjwv/?view_only=91eb519f6d684637a47d1333c5f8856a). We did not post, however, the stimuli videos to protect the privacy of our male participants.

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Appendix C.

Manuscript 3

Jünger, J., Motta-Mena, N. V., Cardenas, R., Bailey, D., Rosenfield, K. A., Schild, C., Penke, L., & Puts, D. A. (2018). *Do women's preferences for masculine voices shift across the ovulatory cycle*? Manuscript submitted for publication. Preprint retrieved from psyarxiv.com/k9y7s DOI: 10.17605/OSF.IO/K9Y7S

Supplementary material and open data are available at https://osf.io/a6byr/

Do women's preferences for masculine voices shift across the ovulatory cycle?

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Declaration of interest: The authors have no conflict of interest to declare.

Abstract

Are estrous mate preference shifts robust? This question is the subject of controversy within human evolutionary sciences. For nearly two decades, mate preference shifts across the ovulatory cycle were considered an important feature of human sexual selection, directing women's attention towards mates with indicators of "good genes" in their fertile phase, when conception is possible. However, several recent studies on masculine faces, bodies and behaviors did not find evidence supporting this account, known as the *good genes ovulatory shift hypothesis*. Furthermore, evidence that preferences for masculine characteristics in men's voices are related to women's cycle phase and hormonal status is still equivocal. Here, we report two independent within-subject studies from different labs with large sample sizes (N = 202 tested twice in Study 1*;* N = 157 tested four times in Study 2) investigating cycle shifts in women's preferences for masculine voices. In both studies, hormonal status was assessed directly using salivary assays of steroid hormones. We did not find evidence for effects of cycle phase, conception risk, or steroid hormone levels on women's preferences for masculine voices. Rather, our studies partially provide evidence for cycle shifts in women's general attraction to men's voices regardless of masculine characteristics. Women's relationship status and self-reported stress did not moderate these findings, and the hormonal pattern that influences these shifts remains somewhat unclear. We consider how future work can clarify the mechanisms underlying psychological changes across the ovulatory cycle.

Keywords: steroid hormones, fertility, attractiveness, voice masculinity, mate preferences, ovulatory cycle

Introduction

Whether women's mate preferences change across the ovulatory cycle has been a central question in the human evolutionary sciences over the last decades. While it seems robust that women experience greater levels of sexual desire and interest when fertile (e.g. Arslan et al., 2018; Jones et al., 2018b; Roney & Simmons, 2013; 2016), it remains unclear if any mate preference shifts exist. Recent studies have cast doubt on the existence of cycle shifts in preferences for masculine faces, bodies and behavioral displays (e.g. Jones et al., 2018a; Jünger et al., 2018a; 2018b; Marcinkowska et al., 2016; 2018a; Muñoz -Reyes et al., 2014), and called attention to methodological criticisms of previous studies. Inconsistencies in the literature are reflected, for instance, in the outcome of two recent meta-analyses, which reached opposite conclusions about whether women's ovulatory cycle phase reliably influences their judgments of men's attractiveness (Gildersleeve et al., 2014a; Wood et al., 2014). In the current manuscript, we tested cycle shifts in women's preferences for masculine voices in two large within-subjects studies from different labs, using natural as well as manipulated voice recordings as stimuli, and also examined hormone concentrations and possible moderator variables.

Theoretical background

Systematic changes in women's sexual interests across the ovulatory cycle have been intensively investigated. In several studies, women experienced heightened sexual interest during their fertile phase, compared to their non-fertile phases (most notably the luteal phase). More precisely, when fertile, women reported higher extra-pair desire (Gangestad et al., 2002; 2005; Grebe et al., 2016; Haselton & Gangestad, 2006; Shimoda et al., 2018), in-pair as well as extra-pair desire (Arslan et al., 2018; Roney & Simmons, 2016) or general sexual desire (Jones et al., 2018b; Roney & Simmons, 2013), which was also found to be linked to their ovarian hormone levels (Jones et al., 2018b; Roney & Simmons, 2013; 2016). To describe differences in sexual psychology and behavior on fertile vs. non-fertile days, Thornhill and

Gangestad (2008) proposed the concept of *dual sexuality*. While sexual behavior outside the fertile phase may have evolved for pair-bonding purposes (Grebe et al., 2016), the most direct benefit for sexual behavior within the fertile phase is conception (Roney & Simmons, 2013). Women are thus predicted to change their mate preferences across the ovulatory cycle. When fertile, their sexual interests should hypothetically be directed preferentially towards mates who possess indicators of high genetic quality to achieve fitness benefits for their offspring (Haselton & Gangestad, 2006). In contrast, sexual interests within the non-fertile phases should be directed to long-term mates with a high potential and willingness to provide parental effort (Gildersleeve et al., 2014a; Thornhill & Gangestad, 2015). Since ovulatory shifts are predicted to aid in obtaining good genes, potentially from extra-pair copulations (Pillsworth & Haselton, 2006), we will further call this concept the *good genes ovulatory shift hypothesis* (GGOSH; Arslan et al., 2018).

Previous studies found evidence for the GGOSH: in the fertile (late follicular) phase, women reportedly shift their preferences toward putative indicators of men's genetic quality, including masculine, dominant-appearing faces (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), voices (Feinberg et al., 2006; Pisanski et al., 2014; Puts, 2005; 2006), bodies (Gangestad et al., 2007; Little et al., 2007), odor (Gangestad & Thornhill, 1998; Havlíček et al., 2005; Thornhill et al., 2013) and behavioral displays (Gangestad et al., 2004; 2007).

However, some purported indicators of good genes are controversial because reported findings challenge the hypothesis that they actually signal heritable fitness benefits and immunocompetence (Scott et al., 2012; 2014; Simmons et al., 2011; Wood et al., 2014). Additionally, the GGOSH itself has been questioned in recent research (Havlíček et al., 2015; Roney & Simmons, 2017). Moreover, several studies raise skepticism about the robustness of preference shifts because of higher powered null replications of prior findings for masculine or symmetrical faces (Harris, 2011; 2013; Jones et al., 2018a; Marcinkowska et al., 2016; 2018a; Muñoz -Reyes et al., 2014; Peters et al., 2009), bodies (Jünger et al., 2018b;

Marcinkowska et al., 2018a; Peters et al., 2009), and behaviors (Jünger et al., 2018a). Furthermore, two large recent studies suggest that women's attraction to men in general, rather than their mate preferences, shifts across the ovulatory cycle (Jünger et al., 2018a; 2018b). Additionally, two meta-analyses analyzing mostly the same datasets (Gildersleeve et al. 2014a; Wood et al. 2014) came to opposite conclusions regarding ovulatory cycle shifts in women's mate preferences, although the methods of Wood and colleagues (2014) have been criticized (Gildersleeve et al., 2014b; Motta-Mena & Puts, 2017). Given this mixed pattern of findings and the centrality of putative ovulatory shifts in current theorizing about human sexual selection, it is clear that there is an urgent need for further research to determine a) the nature of any shifts in women's preferences for masculine features over the ovulatory cycle, and b) the hormonal correlates of any cycle shifts in women's mate preferences.

Preference shifts for voice masculinity

Human voices are highly sexually dimorphic. Sexual dimorphism in vocal anatomy may have been favored by sexual selection because low frequency male vocalizations intimidate rivals and/or attract females (Puts et al., 2016). Masculine voices are characterized by both a lower fundamental frequency and lower, more closely spaced formant frequencies. Fundamental frequency (F_0), the rate of vocal fold vibration during phonation, is the acoustic measure closest to what we perceive as pitch. In males, F_0 is related to testosterone throughout pubertal development (Butler et al. 1989; Harries et al., 1997; 1998; Hodges-Simeon et al., 2015) and during adulthood (Dabbs & Mallinger, 1999; Evans et al., 2008; Puts et al., 2012; 2016). Lower and more closely spaced formant (resonant) frequencies indicate a longer vocal tract and have also been shown to independently increase perceived masculinity (Collins, 2000) and dominance (Cheng et al., 2016; Puts et al., 2006; 2007; Tusing & Dillard, 2000). In such research, formants are often summarized by the composite metric formant dispersion (D_f, the average distance between consecutive formant frequencies computed across the first N, usually four, formants). Hence, the GGOSH would suggest that fertile women should be especially attracted to men with lower F_0 and lower D_f. If preference shifts across the ovulatory cycle for masculine voices occur, then they should be mediated by ovarian hormonal changes. Previous studies report that estradiol, progesterone and the estradiol-to-progesterone-ratio (henceforth *E/P*) are likely candidates for mediating changes in women's mate preferences for voice masculinity over the cycle (e.g. Feinberg et al., 2006; Pisanski et al., 2014; Puts et al. 2013). Estradiol peaks in women's late follicular (fertile) phase and exhibits a smaller increase during the mid-luteal phase. Progesterone levels are usually lower throughout the follicular phase and increase in the luteal phase.

Surprisingly, although null effects for masculine voices in previous studies were attributed to an underpowered analysis (Gildersleeve et al., 2014a), there is a lack of published large, high-powered, within-subject studies investigating preference shifts for masculine voices. However, there are three prior studies that investigated possible cycle shifts for masculine voices and interpreted their results as evidence for mate preference shifts across the ovulatory cycle: Puts (2005) conducted a between-subject study with $N = 136$ female participants ($n = 38$ in the fertile group, $n = 98$ in the non-fertile group) who rated the attractiveness of men's voice recordings, manipulated (raised or lowered) in both F_0 and D_f (see also Puts et al., 2006). Women's conception risk was assessed as a continuous measure via backward counting, but then participants were categorized to cycle phases. Results showed significant cycle shifts: Women preferred men's lowered pitch voices only when they rated them in their fertile phase and for potential short-term relationships ($p = .020$).

Feinberg and colleagues (2006) reported a within-subjects study with $N = 26$ female participants who completed four to six testing sessions resulting in a total of 41 fertile phase sessions ($n = 25$) and 86 non-fertile phase sessions ($n = 25$). However, average scores within each phase were used if a woman was tested more than one time per cycle phase. Cycle phase (fertile vs. non-fertile) was classified via backward counting. Participants rated the general attractiveness of voice recordings that were manipulated in voice pitch and formant frequencies. Notably, cycle shifts for masculine voices were reported only when estrone-3-glucuronide concentrations (E3G, the primary urinary metabolite of estradiol) were included as a covariate in the analyses (p = .012), showing that shifts are stronger for women with lower E3G concentrations. Effects were not significant when pregnanediol-3-glucuronide concentrations (P3G, the primary urinary metabolite of pregnanediol) was included as a covariate (p = .063), or in an analysis without covariates (p = .253).

Using a within-subject design with five weekly test sessions per participant, Pisanski and colleagues (2014) reported that changes in estradiol, but not progesterone, trended toward predicting stronger preferences for manipulated masculine voices in a sample of 62 women (p = .055). Crucially, this effect did not reach significance, and the authors also observed no significant effect of progesterone, testosterone or E/P on preferences for manipulated masculine voices.

Taken together, these studies do not provide strong evidence for cycle shifts in preferences for masculine voices. As Gildersleeve and colleagues (2014a) noted, sample sizes tended to be small, with limited test trials in the experimental designs (e.g. 12 trials; Pisanski et al., 2014). In addition, averaging participant ratings of voices (Feinberg et al., 2006; Pisanski et al., 2014) further reduces the statistical power. Moreover, recent research has pointed out additional methodological issues underlying prior cycle shift studies (Blake et al., 2016; Gangestad et al., 2016; Harris, 2013; Shimoda et al., 2018). First, although backward counting was used as a superior means of estimating cycle phase compared to forward counting (Gangestad et al., 2016), authors did not use luteinizing hormone (LH) urine tests to validate the fertile phase estimates, even though a preovulatory surge of LH clearly demarcates dictinct cycle phases. Second, the only study that reported a significant preference shift for masculine voices (Puts, 2005) lacks a direct assessment of steroid hormones to analyze mediating effects. Third, effect sizes or 95% confidence intervals of the observed preference shifts were not reported, which makes the reported effects harder to interpret. One would expect cycle shift effect sizes to be rather small (Jünger et al., 2018b), but since previous studies worked with relatively small sample sizes, they may not have had the statistical power to reveal such effects. Consequently, published effects might have been false positives or due to publication bias. Fourth, previous studies used manipulated voices or a combination of manipulated and natural voice recording (Puts, 2006) rather than natural voice recordings alone. It is up for debate to what degree computer-manipulated voices have ecological validity, but in any case natural voices should also be used to ensure that results can be transferred to real-life mate preferences. Considering all of these potential methodological problems and the incongruence in reported results, the associations between women's ovulatory cycle, steroid hormone levels, and mate preferences for masculine voices remains unclear.

Overview over the present studies

In the present studies, we aim to clarify a) whether women's attraction to and/or preferences for masculine voices shift across the ovulatory cycle, b) which hormonal changes might underlie these shifts, and c) which moderators influence these shifts. In what follows, we report two large, independent studies from different labs at two different institutions. Both studies employed a within-subjects design with large sample sizes, direct hormonal assessments across one (Study 1) or two (Study 2) ovulatory cycles, and backward counting methods to estimate women's fertility. Study 1 included ovarian hormones (estradiol, progesterone and their ratio), and used voice recordings that were manipulated in F_0 and D_f, while Study 2 included estimated cycle phase (validated with LH tests) as a dichotomous measure of fertility, ovarian hormones as possible mediators, and used natural stimuli. Women's relationship status and self-reported stress are tested as possible moderator variables of ovulatory cycle shifts in women's preferences in Study 2. Additionally, Study 2 was pre-registered[1]; open data and material for both studies can be found at the Open Science Framework (https://osf.io/a6byr).

Study 1

Method

Participants

A total of 202 women ages 18 to 27 years (*M* = 19.56 years; *SD* = 1.59) participated in this study as part of a larger study at Michigan State University. All participants were exclusively or predominantly heterosexual and normally cycling (e.g. not taking any hormonal contraception[2]). They were recruited via print advertisements and the MSU Psychology Department undergraduate subject pool. Informed consent was obtained from participants using procedures approved by the Institutional Review Board of Michigan State University. Participants were scheduled for two laboratory sessions according to self-reported ovulatory cycle length and date of the beginning of last menstrual onset. One laboratory session was scheduled within one day of expected peak estradiol production during the fertile phase, and the other session was scheduled within two days of expected peak progesterone production (mid-luteal phase), as follows: First, information on women's average cycle length and the beginning day of their last menstrual bleeding was collected online before the participant's first session was scheduled. Second, we used this information to estimate the date of their next midcycle LH peak (assuming that the LH peak occurs 15 days prior to the beginning day of their next menstrual bleeding). Third, we used the methods in Puts (2006) to estimate the days of peak estradiol and progesterone levels (approximately the day before the estimated LH peak and 7 days after, respectively). Finally, we scheduled their follicular phase

[1] This pre-registration (can be found at https://osf.io/egjwv) also contained further hypotheses that are not part of the present paper.

[2] Because other conditions, such as pregnancy or endocrine disorders, can also greatly affect women's hormone levels, we scanned our participant's hormone levels for arbitrary values. All values were in line with previously published level ranges from studies with daily hormone assessments (Connor et al., 1981; Marcinkowska et al., 2018) and below progesterone levels that might indicate pregnancy (Connor et al., 1981), suggesting that current pregnancy or endocrine disorders were rather unlikely.

session within one day of their presumptive estradiol peak (i.e., the day of, the day before, or the day after), and we scheduled their luteal phase session within 2 days of their presumptive peak in progesterone. Session order was counterbalanced across participants, such that half of the participants started in their presumed fertile phase and the other half in their presumed luteal phase. Sessions occurred between 1:00 PM and 4:00 PM in order to minimize the influence of circadian hormonal fluctuations.

Saliva collection and hormonal analysis

Approximately 9 ml of saliva was collected from each participant in sodium azide-treated polystyrene test tubes. Participants were asked not to eat, drink (with the exception of plain water), smoke, chew gum, or brush their teeth for at least 1 hour prior to each session to avoid contamination of saliva samples. To stimulate saliva flow, participants rinsed their mouths with water, and were provided with a piece of sugar-free Trident chewing gum (inert in salivary hormone assays). The tube was capped and left upright at room temperature for 18–24 h to allow mucins to settle. Tubes were then frozen at − 20 °C until analysis by the Neuroendocrinology Assay Laboratory at the University of Western Ontario, Canada. Progesterone was assayed using 125I Coat-A-Count assay kits (Diagnostic Products Corporation, Los Angeles, CA) modified for use with saliva (e.g. as in Hampson et al., 2005; Oinonen & Mazmanian, 2007). Similar to previous research (e.g., Finstad et al., 2009), estradiol was assayed using 125I Ultra-Sensitive E2 RIA DSL-4800 kit (Diagnostic Systems Laboratories, Webster, TX) modified for use with saliva. Each sample was assayed twice to verify replicability, and average hormone levels for each sample were used in our analyses. Assay sensitivities were 0.65 pg/ml and 5 pg/ml, and intra-assay coefficients of variation (CV) were 5.1% and 10.7%, for estradiol and progesterone, respectively. Seven participants were excluded from subsequent hormone analysis due to not providing a saliva sample in both sessions, leaving a total of 195 women[3]. Hormone values were positively skewed and thus log10-transformed.

Voice recordings and manipulation

Six male voices were recorded as described in Wolff and Puts (2010), reading an excerpt from a standard voice passage (Fairbanks, 1960). Each voice recording was analyzed and manipulated using Praat (v. 4.4.06; Boersma & Weenink, 2006). Pitch floor and ceiling were 75 Hz and 300 Hz, in accordance with programmers' recommendations; otherwise default settings were used. Formants were measured using the long-term average spectrum (González, 2004; Xue & Hao, 2003), and D_f was computed by taking the average distance between each of the first four formants (Fitch, 1997). For unmanipulated voices, mean F_0 was 109.9 (range = 97.8–122.1, *SD* = 10.0), and mean D_f was 1,003.5 (range = 941.7–1,072.7, *SD* = 51.6). For the current study, each of the six voices was raised and lowered using just-noticeable-difference (JND) parameters from Puts et al. (2007): F_0 was raised and lowered 1.2 semitones, while D_f was manipulated with a 4% change. Thus, from each of the original voices, four versions were produced: raised F_0, lowered F_0, raised D_f, and lowered D_f, for a total of 24 voice recordings. These recordings were distributed into two stimulus sets of 12 recordings, each set comprising 6 raised F_0 with 6 lowered F_0 and 6 raised D_f with 6 lowered D_f.

Procedure

Each participant was seated at a computer station and provided Sennheiser HD280 Pro headphones. The experiment was computerized and participants were instructed using the following script:

"*Please put on the headphones. You are about to hear voice recordings from several men. Please rate how attractive you think each man would be for a short-term, purely*

[3] Excluding another *n*= 15 women who reported cycle lengths less than 25 days or greater than 35 days did not change any results.

sexual relationship, such as a one-night stand (even if you are not interested in such a relationship).”

After listening to each voice recording, participants rated each voice on a 10-point Likert-scale, from “extremely attractive” (coded as 1) to “extremely unattractive” (coded as 10). We reverse-coded the scale for our analyses for an easier understanding of the results. In order to reduce the chance that participants would recognize the voices in each of the voice manipulations, the voice clips were presented in two separate blocks, with an unrelated memory task between each block. Each block consisted of 12 trials with 6 F_0 and 6 D_f manipulations and each speaker represented by one F_0 manipulation and one D_f manipulation. Hence, if for example, in the first block the raised F_0 manipulation was presented for a particular speaker, then the lowered F_0 manipulation was presented in the second block Participants rated all 12 recordings during both laboratory visits in the same order.

Statistical analyses

All analyses in the current manuscript were calculated with the statistic software R 3.4.0 (R Core Team, 2016). The following packages were used: lme4 1.1-13 (Bates et al., 2014), lmerTest 2.0-33 (Kuznetsova et al., 2015), psych 1.7.5 (Revelle, 2016), dplyr (Wickham, 2011).

Results

Ovulatory cycle shifts in women’s mate attraction

First, we tested whether ratings were generally related to ovarian hormone levels or estimated conception risk[4], independent of voice manipulations, in three separate models. All models included attractiveness ratings as the dependent variable, and a random intercept per female rater as well as for male stimulus. Model 1 included estradiol (E) and progesterone (P),

[4] Methods and results for the conception risk analyses can be found in the supplementary material. Ratings did not differ with variation in women’s estimated conception risk, no interaction between F_0 or D_f manipulations and estimated conception risk were observed.

and Model 2 included E/P as predictors[5]. Results show no effect of estradiol or E/P, but importantly, a significant negative effect of progesterone, suggesting higher ratings on average when progesterone levels were lower (Table 1).

Table 1
Multilevel regression analyses of attractiveness ratings as a function of estradiol and progesterone (Model 1) or E/P (Model 2).

	γ	*SE*	*t*	*P*	*95% CI*
Estradiol	-0.17	0.11	-1.53	.127	[-0.39; 0.05]
Progesterone	-0.23	0.10	-2.25	.024	[-0.43; -0.03]
E/P	0.05	0.08	0.63	.529	[-0.11; 0.22]

Note. All variables had 8,820 observations, (195 participants x 2 test sessions x 12 stimuli x 2 masculinity manipulations – missing values).

Ovulatory cycle shifts in women's mate preferences for masculinized voices

Next, we tested if participants showed preference shifts across the ovulatory cycle for voice pitch or formant dispersion across six separate models (discussed below as Models 3 through 6). Again, female raters and male stimuli were treated as random effects. The first two models included women's hormone levels (estradiol and progesterone), voice manipulation (masculinized vs. feminized F_0 in Model 3, D_f in Model 4), as well as their interaction as fixed effects. Then, we additionally calculated two models including E/P, voice manipulation (masculinized vs. feminized F_0 in Model 5, D_f in Model 6), as well as their interaction as fixed effects. Analyses revealed no significant interactions between hormone levels and F_0 or D_f manipulation (Table 2 and 3), indicating no hormonal regulated preference shifts. Additionally, there were no significant main effects of D_f manipulation, but significant main effects of F_0 (Models 3 and 5), showing that voices with masculinized voice pitch were rated as more attractive than the same voices with feminized voice pitch. For hormone levels, we found a significant negative main effect for progesterone in Model 3 (with manipulated F_0) but not in Model 4 (with manipulated D_f), showing that ratings were higher when progesterone was lower. We, again, did not find a significant effect for estradiol in Model 3 or

[5] We decided to analyze the effect of hormones on ratings in two separate models because of possible problems of multicollinearity (r = .61 for estradiol and E/P; r = -.16 for progesterone and E/P).

Model 4. Additionally, we found a significant main effect of E/P in Model 5 (with manipulated F_0) but not in Model 6 (with manipulated D_f), showing that ratings were higher when E/P was higher.

Table 2
Multilevel regression analyses of attractiveness ratings as a function of estradiol and progesterone levels and manipulated voice pitch (Model 3) or formant dispersion (Model 4).

	γ	*SE*	*t*	*p*	*95% CI*
Voice pitch model					
F_0	-1.75	0.33	-5.29	<.001	[-2.40; -1.10]
Estradiol	-0.01	0.18	-0.03	.975	[-0.37; 0.36]
Progesterone	-0.52	0.17	-3.16	.002	[-0.84; -0.20]
F_0 x Estradiol	-0.20	0.22	-0.92	.358	[-0.64; 0.23]
F_0 x Progesterone	0.18	0.19	0.93	.354	[-0.20; 0.55]
Formant model					
D_f	-0.30	0.32	-0.93	.353	[-0.92; 0.33]
Estradiol	-0.24	0.18	-1.35	.178	[-0.59; 0.11]
Progesterone	-0.02	0.16	-0.94	.347	[-0.47; 0.16]
D_f x Estradiol	-0.00	0.21	-0.00	.997	[-0.42; 0.41]
D_f x Progesterone	0.20	0.18	1.06	.288	[-0.17; 0.56]

Note. F_0 = fundamental frequency (voice pitch), D_f = formant dispersion. All variables in voice pitch model had 4,416 observations, formant model 4,404 observations (each 195 participants x 2 test sessions x 12 stimuli – missing values).

Table 3
Multilevel regression analyses of attractiveness ratings as a function of E/P and manipulated voice pitch (Model 5) or formant dispersion (Model 6).

	γ	*SE*	*t*	*p*	*95% CI*
Voice pitch model					
F_0	-1.77	0.26	-6.82	<.001	[-2.28; -1.26]
E/P	0.29	0.14	2.11	.034	[0.02; 0.56]
F_0 x E/P	-0.19	0.16	-1.14	.253	[-0.51; 0.13]
Formant model					
D_f	-0.13	0.25	-0.53	.599	[-0.62; 0.36]
E/P	-0.02	0.13	-0.14	.893	[-0.28; 0.25]
D_f x E/P	-0.12	0.16	-0.74	.460	[-0.43; 0.19]

Note. F_0 = fundamental frequency (voice pitch), D_f = formant dispersion. All variables in voice pitch model had 4,416 observations, formant model 4,404 observations (each 195 participants x 2 test sessions x 12 stimuli – missing values).

Robustness checks

We conducted further analyses to test the robustness of our results. To ascertain that our results were not driven by order effects of testing sessions or participants' age, we entered session number and participant age in all of our models. The main effect of progesterone from

Model 1 disappeared, but the one from Model 3 and the main effect of E/P from Model 5 remained significant. Moreover, there was a main effect of session number, indicating that ratings were on average higher in the second session (p = .02). However, all other results remained virtually identical (significant main effect for F_0 as well as all non-significant effects) and can be found in the supplement (Tables S2 – S7). Next, according to a possibly occurring carryover effect of women's hormonal state in the first session that might influencing the ratings in the second session (Wallen & Rupp, 2010), we repeated all analyses including an interaction between session number and hormone levels. Results revealed no interaction between session number and estradiol levels (p = .91) or session number and E/P (p = .15), but a significant interaction between session number and progesterone levels (p = .02), indicating that ratings were higher in the second session, only when progesterone levels were lower. However, this interaction was not robust in all models. Importantly, all interactions between hormone levels and masculine cues remained non-significant, details can be found in the supplement (Tables S8 – S11).

Study 2

Study 2 was conducted at the University of Goettingen, Germany, independently from Study 1, and differed from Study 1 in several ways. First, Study 2 used unmanipulated voice recordings as stimuli, which enabled us to explore preferences for other acoustic parameters, including jitter and shimmer (cycle-to-cycle variation in F_0 and amplitude, respectively), which are associated with pathological voice quality (Dejonckere et al., 1996; Michaelis et al., 1998). Second, baseline testosterone levels of the men who provided the voice stimuli were assessed along with the other vocal cues. This provided a direct test of whether preference shifts occur for men with higher baseline testosterone levels, which are generally found to be negatively associated with F_0 (Butler et al., 1989; Dabbs & Mallinger, 1999; Harries et al., 1997, 1998). Third, in addition to estradiol and progesterone, participants' testosterone and cortisol levels were also assessed. Like estradiol, testosterone can show mid-cycle peaks and has been found to predict women's preferences for masculine faces (Bobst et al., 2014; Welling et al., 2007). Recent research also suggests that cortisol and psychological stress should be measured in studies on hormones and female mate preferences. Stress elevates cortisol levels (Herrera et al., 2016), which may inhibit estradiol production in young women (Roney & Simmons, 2015) and decrease women's preferences for male facial masculinity (Ditzen et al., 2017, but see Jones et al., 2018a). Fourth, we ascertained women's relationship status. Recent studies reported ovulatory cycle shifts in attraction to men (Jünger et al., 2018a; 2018b) and in sexual desire (Roney & Simmons, 2016) that were evident only in partnered women. Furthermore, partnered women were found to be more likely to have sexual fantasies about men other than their primary partner (Gangestad et al., 2002), rate the odor of dominant men as sexy (Havlíček et al., 2005), and report stronger masculinity preferences than singles (Jones et al., 2018a). By contrast, Jones and colleagues (2018b) reported no evidence for a moderating effect of women's relationship status on general sexual desire. The lack of converging evidence in the literature emphasizes the need for further analyses to evaluate the influence of women's relationship status on cycle shifts in preferences and attraction. Fifth, we used cycle phase (validated with LH tests) as a categorical measure, and all participants were investigated in four testing sessions across two ovulatory cycles each (see below for detailed methods). Sixth, besides assessing sexual attractiveness ratings, we also assessed long-term attractiveness ratings for all stimuli.

Pre-registered Hypotheses and Research Questions

Following previous findings of ovulatory cycle shifts in mate preferences, we hypothesize that women in the fertile phase, compared to their luteal phase, will evaluate men's voices as more attractive for short-term sexual relationships (Hypothesis 1). This effect should be mediated by changes in the steroid hormones estradiol and progesterone (Hypothesis 2). Hormone levels of testosterone and cortisol will be analyzed as possible mediators in an exploratory manner. Building on previous studies, we derived cues for which cycle shifts in mate preferences, if existent, should occur: Women in their fertile window should be more sexually attracted to men with a lower fundamental frequency and formant dispersion, as well as a higher baseline testosterone level, compared to low-fertility days of their cycle (Hypothesis 3a). We predict these findings to be robust when controlling for men's age. We will furthermore analyze women's preferences for the voice parameters jitter and shimmer in an exploratory manner. We also state the alternative hypothesis that women in their fertile window, compared to their luteal phase, will not show cycle shifts in their mate preferences regarding men's voice attractiveness for sexual relationships (Hypothesis 3b). One possible moderator for cycle shifts might be women's relationship status. Since it remains unclear if both single and partnered alter their mating strategies across the cycle, we state two alternative hypotheses: Cycle phase shifts in preferences for short-term mates are larger for partnered women than for single women, or, alternatively, the participant's relationship status does not affect the strength of cycle phase shifts in preferences for short-term mates (Hypotheses 4a and 4b). Moreover, we hypothesized self-reported stress as a moderator of cycle shifts: Cycle shifts should be attenuated when self-reported stress is high (Hypothesis 5). We also predict, as the GGOSH suggests, that preference shifts should be absent or less pronounced when it comes to long-term mate preferences (Hypothesis 6, see Gildersleeve et al., 2014a).

Methods

Participants and Recruitment

A total of 157 heterosexual female participants (aged 18-35 years, *M* = 23.3, *SD* = 3.4), out of 180 recruited, finished all sessions and were therefore included in further analyses (this sample is the same as in Jünger et al., 2018a and 2018b). Seventeen women who attended only the introductory session of the study dropped out before participation (six fulfilled one of the exclusion criteria below, four quit the study without further reasons, four did not respond to emails, three had scheduling problems). Another six dropped out during the study because of completing only the first testing session (four had scheduling problems, two did not respond to emails after the first session). Based on the inclusion criteria of other ovulatory cycle studies, our participants had to fit the following preregistered criteria: female, between 18 and 30 years[6] old, naturally cycling (no hormonal contraception for at least three months, not expected switch to hormonal contraception during the study, no current pregnancy or breastfeeding, no childbirth or breast-feeding during the previous three months, not taking hormone-based medication or anti-depressants). Additionally, participants had to report that their ovulatory cycles had a regular length between 25 and 35 days during the last 3 months. At the beginning of the study, 75 of the participants reported being in a relationship, 82 reported being single. Upon completion of all sessions, participants received a payment of 80€ or course credit, and a 3D printed figure of themselves.

Procedure

All participants took part in five individually scheduled sessions that were scheduled between May 2016 and March 2017. In the first session participants received detailed information about the general procedure, duration of the study and compensation. All participants signed a written consent document, and the ethics committee of the Institute of Psychology at the University of Goettingen approved the protocol. The experimenter explained the ovulation tests and checked the inclusion criteria. To count the days to the next ovulation and plan the dates of the experimental sessions, cycle length as well as the dates of the last and the next menstrual onset were assessed. Finally, demographic data were collected.

Sessions two to five, the computer-based testing sessions, took place across two ovulatory cycles (approx. two months) per participant, once per cycle during the late follicular (fertile) phase and once during the luteal phase. To control for possible effects of diurnal changes in hormone levels, all sessions took place in the second half of the day (mainly

[6] One of the participants reported being 35 years old. We excluded her data in the main analyses, but included it in the robustness checks because she met all other inclusion criteria and had positive LH tests. Including her data did not alter the results.

between 11.30 am and 6 pm). When arriving at the lab, participants first completed a screening questionnaire, assessing their eligibility and some control variables for the saliva samples (Schultheiss & Stanton, 2009). Next, the saliva samples were collected via passive drool before the participants started their first rating task[7]. In preparation for listening to the unmanipulated voice recordings, participants were instructed to evaluate the men's attractiveness as they perceived it "in that moment", independent of their own current relationship status or general interest in other men. Participants were then presented with the voice recordings in a randomized order. After listening to a voice, participants rated it for sexual attractiveness (assessing short-term attractiveness) and for long-term attractiveness using an eleven-point Likert scale from -5 (*extremely unattractive*) to +5 (*extremely attractive*). Definitions of sexual attractiveness and attractiveness for a long-term relationship were provided prior to the ratings and read as follows:

a) *Sexually attractive*: Men who score high would be very attractive for a sexual relationship that can be short-lived and must not contain any other commitment. Men scoring low would be very unattractive for a sexual relationship.
b) *Attractive for a long-term partnership*: Men who score high would be very attractive for a committed relationship with a long-term perspective. Men scoring low would be very unattractive as a long-term partner.

After each session, the appointment for the next session was arranged individually based on participant's ovulatory cycle.

Furthermore, all participants of the current study were asked to participate in a separate daily online diary study (Arslan et al., 2016) that was conducted in parallel to the described lab study. Within this diary study, participants had to fill out a questionnaire about

[7]The described study on ovulatory cycle shifts for voice masculinity was one part of a larger study (see pre-registration). Participants also had to complete other rating tasks and anthropometric data was collected between these tasks. The duration of one experimental session was approximately 2-2.5h.

daily feelings and behavior across 70 days. We used the stress ratings from this study for further analyses (see below).

Measures

Ovulatory cycle phase

Women's cycle phase was determined by the reverse cycle day method, based on the estimated day of the next menstrual onset (Gildersleeve et al., 2012) and confirmed by highly sensitive (10 mIU/ml) urine ovulation test strips from purbay®, which measure luteinizing hormone (LH). These LH tests were conducted privately at home on the estimated day of ovulation and the four days prior to that, and results were self-reported by the participants. The study investigated two ovulatory cycles in which every participant reported to the lab twice: Once while being fertile (at the days prior to ovulation, usually reverse cycle days 16-18, with reverse cycle day 16 as the ideal date) and once when not fertile (during the luteal phase, after ovulation and prior to the next menstrual onset, usually reverse cycle days 4-11, with reverse cycle days 6 to 8 as the ideal dates). An Excel sheet was used to compute the acceptable days for the testing sessions and track whether a participant started in her fertile or luteal phase. Of all participants who finished all sessions, 66 participants started with the first session in their luteal phase, and 91 started in the fertile phase.

For the main cycle phase analyses, we excluded a total of 45 participants due to negative LH tests in both cycles, irregular ovulatory cycles or inappropriate scheduling of testing sessions (see "Preliminary Analyses" for more details), resulting in n = 112 women. Of these participants, 46 started with the first session in their luteal phase, and 66 started fertile. However, all 157 women were included in the denoted robustness checks.

Hormone measures

We collected four saliva samples from each participant (one per testing session) prior to the rating tasks. Contamination of saliva samples was minimized by asking participants to abstain from eating, drinking (except plain water), smoking, chewing gum or brushing teeth for at least one hour before each session. The samples were stored at -80°C directly after collection until shipment on dry ice to the Kirschbaum Lab at Technical University of Dresden, Germany, where estradiol, progesterone, testosterone and cortisol were assessed via liquid chromatography mass spectrometry (LCMS; Gao et al., 2015). Because the LCMS analysis of estradiol detected only 22% of all possible values, the samples were reanalyzed using the highly sensitive 17β-estradiol enzyme immunoassay kit (IBL International, Hamburg, Germany). These latter estradiol values were used in subsequent analyses. Hormone levels were skewed, therefore, we centered all hormone values on their subject-specific means and scaled them afterwards (i.e. divided them by a constant), so that the majority of the distribution for each hormone varied from -0.5 to 0.5 to facilitate calculations in the linear mixed models (as in Jones et al., 2018b; and congruent with our approach in Jünger et al., 2018a; 2018b). This is a common procedure to isolate effects of within-subject changes in hormones, avoiding the influence of outliers on results and dealing with the non-normal distribution of hormone levels. Hormone levels were nearly normally distributed afterwards, a figure showing the distribution of hormone levels after this procedure can be found in the supplement (Figure S1). Importantly, this procedure did not change any findings compared to analyses with untransformed hormone values. The R code for this procedure can be found in the open script.

Stimuli and masculinity analyses

Seventy-six voices of different men, counting from three to eight in German, recorded as part of the Berlin Speed Dating Study (see Asendorpf et al., 2011 for more details), were presented via headphones (JVC® HA-RX300). We selected recordings from 76 participants out of a pool of 382 by gender (male) and age (between 18 and 30 years old, matching the age of the eligible female participants in the study). Stimulus males' baseline testosterone levels were measured from saliva samples. The samples were analyzed using radioimmunoassay by the Kirschbaum lab at the Technical University Dresden. Each recording was analyzed using

Praat software (version 6.0.17). Pitch, floor, ceiling and other settings were set in line with Study 1. Across each recording, we measured mean F_0 (henceforth, F_0; M = 110.74, range = 85.30–157.48; SD = 12.66) and median formant frequencies from which we computed D_f (M = 1043.19 Hz, range = 961.67–1137.68, SD = 30.30 Hz) as in Study 1, and measured four measures of jitter and five measures of shimmer. All jitter (r > .97) and shimmer (r > .31) variables were correlated and therefore *z*-standardized and summed (jitter: M = 0.00, SD = 0.99; shimmer: M = -0.02, SD = 0.84). Additionally, we computed formant position (P_f; M = 0.00, range = -1.36–2.96, SD = 0.68), the standardized formant value for the first four formants which has been found to be more sexually dimorphic than D_f (Puts, Apicella, & Cardenas, 2012).

Stress ratings

Self-reported stress was measured with one item ("*Today I was stressed out*") on a five-point Likert-scale (from "*less than usual*" to "*more than usual*") on a daily basis within the accompanying online diary study (see above) with planned missings[8]. For the analysis, the stress value from the day of the lab testing session was used. If there was no existing value for that specific day, then we averaged the values of the two days before and after the testing day, if available. In total, 54 of the 157 participants were excluded from analyses, 26 because they did not take part in the diary study, 20 because they did not fill out enough days to provide data for at least one fertile and one luteal session, and eight because they took part in the study at another time window (not parallel to the lab study). Sixty-two participants had stress data for at least one fertile and one luteal session, and 41 for all sessions, resulting in an available dataset of 160 cycles (out of 314 possible cycles; 119 cycles out of 224 for n = 112) in total.

[8] The participants had to fill out more than 100 items per day. Therefore, we decided to reduce the daily items by planned missings to minimize dropouts while obtaining sufficient data for each item. The relevant stress item was shown on about 40% of all days.

Results

Preliminary Analyses

First, we counted how many cycles were irregular, so that the day of the testing session was scheduled more than three days apart (before or after) from the defined windows of appropriate testing days (e.g. fertile sessions were defined as being appropriate within reverse cycle days 15-18, luteal sessions were defined as being appropriate within reverse cycle days 4-11, see section “ovulatory cycle phase”). Even though all participants reported having regular ovulatory cycles in the introductory session, eight women had irregular cycles in both investigated cycles, and 32 reported one cycle being irregular, resulting in 48 out of 314 (15.3%) cycles being irregular. Next we checked how many of the participants’ ovulatory cycles had positive LH tests (indicating a LH surge) in the estimated fertile phase to detect non-ovulatory cycles. Twelve participants reported negative LH test results for both investigated cycles, nine reported negative LH tests results for one cycle. In total, the LH tests in 33 of all 314 cycles (10.5%) were negative. Additionally, we checked the temporal relationship between the reported day of LH surge and the date of scheduled testing session. Because ovulation usually occurs within 24-36 hours after the observed LH surge, testing sessions that were scheduled more than two days after the surge might have already been in the early luteal phase. Out of the 281 cycles for which an LH surge was observed, thirteen (4.63%) purportedly fertile phase sessions were scheduled three or four days after the LH surge. Therefore, 268 (95.37%) were scheduled within an appropriate range of three days before to two days after the LH surge (in total: M = -0.12, SD = 1.39 days in relation to the day of the observed LH surge). A histogram showing the distribution of days of fertile phase testing sessions relative to the observed LH surge can be found in the supplement (Figure S2). Participants with irregular cycles, negative LH tests or the risk of early luteal phase instead of fertile phase testing session were excluded in the main analyses, but included in denoted robustness checks.

Main analyses: Cycle shifts in women's attraction and mate preferences

We first tested for possible ovulatory cycle shifts in women's attraction to men's voices in general (Hypothesis 1). For the multilevel analyses with attractiveness rating as the dependent variable (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness), female raters as well as the male stimuli were treated as random effects. Women's cycle phase (0 = luteal phase, 1 = fertile phase) was treated as a fixed effect. We additionally let participant's slopes vary systematically across cycle phase by modeling cycle phase as a random slope. This analysis showed a significant cycle shift in women's attraction: Ratings for sexual attractiveness were higher in the fertile phase than in the luteal phase of the ovulatory cycle ($\gamma = 0.10$, $SE = 0.05$, $t = 2.14$, $p = .035$, $95\%CI = [0.01; 0.19]$), supporting Hypothesis 1. We didn't observe differences between fertile phase and luteal phase ratings for long-term attractiveness ($\gamma = 0.06$, $SE = 0.04$, $t = 1.45$, $p = .150$, $95\%CI = [-0.02; 0.15]$). These results indicate the existence of ovulatory cycle shifts on women's mate attraction to men's voices for sexual, but not long-term attractiveness, such that, overall, fertile women rated men's voices as being more attractive[9].

To analyze whether women's mate preferences for specific vocal cues change across the ovulatory cycle (Hypothesis 3), we calculated additional three multilevel models. In all models, female participants as well as male vocal stimuli were treated as random effects, women's cycle phase was treated as fixed effect and a random slope for cycle phase varying in participants was included. Moreover, the vocal masculinity cues F_0 (Model 3), D_f (Model 4) and men's baseline testosterone levels (Model 5) were treated as fixed effects separately. Further, because recent research suggests P_f as a superior indicator of vocal masculinity compared to D_f (Puts et al., 2012), we also analyzed possible cycle shifts in mate preferences for men's P_f (Model 6). Results show a significant main effect for cycle phase on sexual

[9] In line with Study 1, we also analyzed possible main effects of hormone values (estradiol and progesterone or E/P) on attractiveness ratings separately in an exploratory manner, as they were not part of the preregistration. No significant effects were observed. Details can be found in the supplementary material (Tables S18 – S19).

attractiveness ratings in each model[10] (Table 4), again supporting Hypothesis 1. Women rated men's voices as more attractive when they were fertile. Moreover, there was a significant effect of fundamental frequency and one of formant dispersion on attractiveness ratings: Voices with lower F_0 and voices with lower D_f were rated as more attractive. The effects of P_f or baseline T did not reach statistical significance. We observed a significant interaction effect between cycle phase and baseline T, indicating that fertile women rate lower T men as more attractive, which is the opposite direction as stated in Hypothesis 3. None of the other vocal cues interacted with cycle phase, indicating that women's mate preferences do not shift for specific cues in men's voices across the ovulatory cycle[11], in contrast to Hypothesis 3. Results remained stable when controlling for men's age. Moreover, results remained virtually identical when adding all four vocal masculinity cues to the same model at the same time, details can be found in the supplement (Tables S16 and S17).

[10] Regarding the length of our manuscript, we decided to report all other results for the long-term attractiveness ratings in the supplementary material (Tables S12 – S15), during the review process. Results for long-term ratings all showed null results for preference shifts across the cycle, hence, all results were supporting Hypothesis 6.

[11] In line with Study 1, we also analyzed possible interaction effects of hormone values (estradiol and progesterone or E/P) with all masculine vocal cues (F_0, D_f, P_f, baseline T) separately in an exploratory manner. None of these models revealed any significant interaction effect, again suggesting no preference shifts for masculine voices. Details can be found in the supplementary material (Tables S28 – S31).

Table 4

Multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase and men's voice pitch, formant dispersion, formant position or baseline testosterone levels.

	γ	*SE*	*t*	*p*	*95% CI*
F0 model					
Cycle phase	0.10	0.05	2.14	.035	[0.01; 0.19]
Men's F_0	-0.68	0.12	-5.71	<.001	[-0.92; -0.45]
Cycle phase x men's F_0	0.01	0.02	0.55	.586	[-0.03; 0.06]
Df model					
Cycle phase	0.10	0.05	2.14	.035	[0.01; 0.19]
Men's D_f	-0.28	0.14	-2.04	.045	[-0.56; -0.01]
Cycle phase x men's D_f	0.02	0.02	0.91	.362	[-0.02; 0.06]
Pf model					
Cycle phase	0.10	0.05	2.14	.035	[0.01; 0.19]
Men's P_f	-0.40	0.21	-1.93	.057	[-0.81; 0.01]
Cycle phase x men's P_f	0.02	0.03	0.52	.600	[-0.05; 0.08]
Baseline t model					
Cycle phase	0.10	0.05	2.14	.035	[0.01; 0.19]
Men's baseline testosterone	0.07	0.14	0.47	.639	[-0.21; -0.35]
Cycle phase x men's baseline testosterone	-0.04	0.02	-2.00	.046	[-0.09; -0.00]

Note. F_0 = fundamental frequency (voice pitch), D_f = formant dispersion, P_f = formant position. All variables had 34,048 observations (112 participants x 4 test sessions x 76 stimuli).

We also analyzed influences of men's jitter and shimmer on attractiveness ratings in an exploratory manner. The main effects of cycle phase stayed significant. We found a significant main effect for shimmer (γ = 0.28, *SE* = 0.14, *t* = 2.04, *p* = .045, *95%CI* = [0.01; 0.56]), suggesting higher ratings when shimmer was high; but not for jitter (γ = 0.07, *SE* = 0.14, *t* = 0.51, *p* = .609, *95%CI* = [-0.21; 0.35]). The interactions of cycle phase with jitter or shimmer were not significant.

Next, we calculated Spearman rank correlations between attractiveness ratings in the fertile and those in the luteal phase to better understand the reported cycle effect. Results from this analysis indicate that ranks of the rated voices (from the most to the least attractive voice) did not differ between the fertile and the luteal phase for sexual attractiveness (r = .99, p < .001). Rather, most of the voices received a slightly better rating in the fertile phase compared to the luteal phase ($M_{fertile}$ = -0.33, *SD* = 1.23, M_{luteal} = -0.40, *SD* = 1.23, *d* = 0.05). These results indicate that women rated the same men as more or less attractive, independent of their cycle phase, suggesting that differential effects of masculinity cues are rather unlikely.

Hormonal influences on cycle phase shifts

In order to analyze whether steroid hormones mediate effects of cycle phase (Hypothesis 2), we entered cycle phase, estradiol, progesterone, E/P, testosterone, and cortisol as fixed effects into the multilevel model with sexual attractiveness ratings as the outcome variable (Model 7), female participants and male stimuli as random effects and a random slope for cycle phase varying in participants. Results demonstrate that, in contrast with Hypothesis 2, there were no mediating effects of any hormone levels: results of cycle phase remained significant and effects were even larger than in the model without hormone levels (see Table 5), reinforcing the effect that ratings increased in women's fertile phase compared to ratings in the luteal phase. Moreover, there was a significant positive effect of progesterone on sexual attractiveness ratings. Counterintuitively, ratings were higher when progesterone levels were higher. There were no significant effects of estradiol, E/P, testosterone, or cortisol. Again, because of possible problems of multicollinearity (significant negative correlation between E/P and progesterone, significant positive correlations between E/P and estradiol, as well as E/P and cortisol, see Table S66 for all correlation coefficients between hormones), we also calculated additional models with estradiol, progesterone, testosterone and cortisol as fixed effects, but excluding E/P. Results remained virtually identical and can be found in the supplemental material (Table S20). However, in line with our reported results in Jünger et al. (2018b), and because results did not change when analyzing hormone values separately, we decided to report the models with all hormones included here.

Table 5
Multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase with hormone levels as possible mediator variables

	γ	*SE*	*t*	*p*	*95% CI*
Cycle phase	0.13	0.06	2.29	.023	[0.02; 0.25]
Estradiol	-0.06	0.05	-1.09	.276	[-0.16; 0.05]
Progesterone	0.11	0.05	2.41	.016	[0.02; 0.20]
E/P	0.01	0.03	0.23	.822	[-0.05; 0.06]
Testosterone	0.01	0.02	0.58	.561	[-0.03; 0.05]
Cortisol	-0.01	0.04	-0.18	.855	[-0.10; 0.08]

Note. All variables had 28,956 observations (112 participants x 4 test sessions x 76 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All hormone values were centered to their subject-specific means and then scaled.

Investigating women's relationship status as a possible moderator

To evaluate whether women's relationship status influences ovulatory cycle shifts[12], we first categorized all women as in a relationship who reported being in an open relationship, in a committed relationship, engaged or married. Relationship status changed for 13 women (for seven of the *n* = 112 cycle phase sample) across the study. Their data were categorized according to their relationship status on the particular testing day. One multilevel model (Model 8) with women's cycle phase and relationship status as fixed effects, a random slope for cycle phase varying in participants, female participants and male stimuli as random intercepts again showed significant main effects of cycle phase (Table 6). Sexual attractiveness ratings were higher in the fertile phase of the ovulatory cycle. There were no significant effects of relationship status or of the cycle phase × relationship status interaction. Therefore, women's relationship status did not moderate the cycle phase effect on attractiveness ratings.

[12] Although we originally stated the hypothesis that women's relationship status might moderate preference shifts, we decided to rather report our moderator analyses for attraction shifts, because we did not find any hint for an observable preference shift in our analyses. However, we also investigated possible three-way interactions between cycle phase, relationship status and all masculine vocal cues (F_0, D_f, P_f, baseline T) separately. None of these models revealed any significant interaction effect, indicating no compelling evidence for preference shifts for masculine voices and no moderation effects of women's relationship status, in contrast to Hypothesis 4a, but supporting Hypothesis 4b. Details can be found in the supplement (Tables S32 – S33).

Table 6
Multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase and women's relationship status.

	γ	*SE*	*t*	*p*	*95% CI*
Cycle phase	0.13	0.06	2.04	.044	[0.01; 0.25]
Relationship status	-0.12	0.09	-1.31	.189	[-0.30; 0.06]
Cycle phase x Relationship status	-0.05	0.09	-0.62	.537	[-0.22; 0.12]

Note. All variables had 34,048 observations (112 participants x 4 test sessions x 76 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile, and relationship status with 0 = single, 1 = in a relationship.

Self-reported stress

Furthermore, we analyzed whether self-reported stress moderated the relationship between cycle phase and attractiveness ratings. We calculated one further multilevel model (Model 9). Again, female raters as well as the male stimuli were treated as random effects. Women's cycle phase and self-reported stress ratings were treated as fixed effects and a random slope for cycle phase varying in participants was included. Because many women did not fill out the self-reported stress item for every testing day due to the planned missings design (see Methods), data for only about half of the sample were available (119 cycles out of 224 assessed cycles). When evaluating sexual attractiveness ratings as the outcome variable, we found a significant main effect of cycle phase, revealing that attractiveness ratings were higher in the fertile phase of the cycle. However, the main effect of self-reported stress, as well as the interaction between cycle phase and self-reported stress was not significant (Table 7), indicating that there was no moderation effect of self-reported stress on cycle effects.

Table 7
Multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase and women's self-reported stress.

	γ	*SE*	*t*	*p*	*95% CI*
Cycle phase	0.33	0.11	2.95	.003	[0.11; 0.54]
Self-reported stress	-0.03	0.04	-0.73	.467	[-0.10; 0.05]
Cycle phase x Self-reported stress	-0.08	0.05	-1.76	.079	[-0.18; 0.01]

Note. All variables had 18,088 observations (75 participants x 4 test sessions x 76 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile.

Further robustness checks and exploratory analyses

Besides the exploratory analyses we have already reported in footnotes, we conducted further analyses to test the robustness of our effects. To rule out the possibility that the main effect results were driven by order effects of testing sessions (in particular, participating in the first session when fertile; Suschinsky et al., 2014; Wallen & Rupp, 2010), we controlled for initial cycle phase in our analyses. The effect of cycle phase remained stable (γ = 0.10, *SE* = 0.05, *t* = 2.14, *p* = .035, *95%CI* = [0.01; 0.19]). Moreover, initial cycle phase affected sexual attractiveness ratings (γ = 0.36, *SE* = 0.15, *t* = 2.48, *p* = .014, *95%CI* = [0.07; 0.66]), in that ratings were higher when participants started in the fertile phase. We also controlled our analyses for session number. Again, the effect of cycle phase remained stable (γ = 0.10, *SE* = 0.05, *t* = 2.03, *p* = .045, *95%CI* = [0.00; 0.18]) and session number affected sexual attractiveness ratings (γ = -0.04, *SE* = 0.01, *t* = -3.61, *p* <.001, *95%CI* = [-0.06; -0.02]), in that ratings decreased on average by number of the testing session.

Then, to investigate if being tested while fertile in the first session affects ratings in later sessions, we calculated an additional model including an interaction between session number and initial cycle phase. We found a significant interaction between session number and initial cycle phase (γ = -0.07, *SE* = 0.02, *t* = -3.33, *p* <.001, *95%CI* = [-0.12; -0.03]), showing that ratings decreased by ongoing testing sessions when the initial session was fertile, but not when the initial session was scheduled in the luteal phase. Additionally, there was a main effect of initial session (γ = 0.57, *SE* = 0.16, *t* = 3.68, *p* <.001, *95%CI* = [0.26; 0.89]), indicating higher ratings when the first session was fertile, but no main effect of session number (γ = 0.00, *SE* = 0.02, *t* = 0.14, *p* = .892, *95%CI* = [-0.03; 0.04]). Based on these findings, to rule out that our null results for cycle shifts in mate preferences were caused by a carryover effect of the hormonal state in the initial session, we also controlled our main preference shifts models for an interaction effect between session number and initial cycle phase. Results remained virtually identical and can be found in the supplementary material (Table S65).

Next we conducted our analyses with all recruited women[13] (*N* = 157) including (Tables S21 – S25) or excluding random slopes (Tables S60-S64). Nearly all results remained robust across all checks. However, the significant interaction of cycle phase and men's baseline testosterone levels (Table S22 and S61) disappeared in all robustness checks. We conducted additional exploratory robustness checks and falsification tests. First, we repeated all of our analyses using sexual minus long-term attractiveness as the dependent variable, to allow for the possibility that differences in estimated effects on sexual- and long-term attractiveness ratings would be difficult to estimate, because of the high correlations between these outcomes (r = .90). This is a very specific prediction of the GGOSH (see e.g. Gangestad et al., 2004; 2007). Complementary to that, we also ran all analyses with sexual plus long-term attractiveness as the dependent variable, which provides a more aggregated estimation of overall attraction (Gangestad et al., 2004; 2007). Importantly, none of the models revealed any observable preference shifts as a function of cycle phase or hormone levels (see Tables S42-S59 in the supplementary material for detailed results). In summary, we did not observe any preference shift in our robustness checks. The estimated effect size of cycle phase on attractiveness ratings was robust across robustness checks and statistically significant in the vast majority of models.

Discussion

We sought to clarify whether women experience hormone related mate preference shifts for male voice masculinity across the ovulatory cycle. We evaluated hormonal influences underlying women's cycle shifts in attraction and preferences for masculine voices and further investigated potential moderators of these effects. We included multiple measures

[13] In the previous versions of this manuscript, we reported these analyses as our main analyses and the analyses with those n = 112 women who perfectly met all inclusion criteria as robustness checks. We decided to switch these analyses during the review process.

(hormone levels assayed from saliva and cycle phase confirmed via LH tests), investigated preferences for natural as well as manipulated stimuli, and employed within-subject designs in two samples that exceed the sizes from previous studies. In both studies, we did not find compelling evidence to support the hypothesis that women experience (hormone related) cycle shifts in mate preferences for masculine voices. Further, we report that progesterone and E/P influenced attractiveness ratings in Study 1, Study 2 indicated the presence of cycle phase shifts in women's overall attraction to men's voices, but not shifts in preferences for specific vocal characteristics. Women's relationship status or self-reported stress did not moderate attraction shifts. We did not find a clear pattern of hormonal influences on attractiveness ratings across the cycle. In the following, we interpret these findings and highlight implications for future research.

Preference vs. attraction shifts

As in previous work evaluating shifts in mate preferences for body and facial masculinity (Jones et al., 2018a; Jünger et al., 2018b; Marcinkowska et al., 2018a; Peters et al., 2009), as well as men's behaviors (Jünger et al., 2018a), we report no observed effects of cycle phase, conception risk or steroid hormone levels on women's mate preferences for masculine voices across two independent studies. Therefore, we did not find compelling evidence for the GGOSH, even with large samples, multiple time points (i.e. greater power to detect an effect across testing sessions), and highly reliable estimates of cycle phases compared to previous studies that purportedly found evidence for mate preference shifts for masculine voices across the ovulatory cycle. Indeed, in one analysis for Study 2, we found an interaction between women's cycle phase and men's baseline testosterone levels on sexual attractiveness ratings, but this effect was in the opposite direction from that predicted by our hypotheses and the GGOSH: Ratings were higher in the fertile phase when men's baseline testosterone was low. However, the effect is counter-intuitive and disappeared in all of our robustness checks. We therefore suggest that it is a false positive. Hence, we interpret our findings as null results for mate preference shifts across the cycle. These results and recent studies reporting null results cycle shifts for body or behavior preferences (Jünger et al., 2018a; 2018b; Marcinkowska et al., 2018a) indicate that it no longer appears to be the case that null results are specific to face preferences (e.g. Jones et al., 2018a; Muñoz-Reyes et al., 2014; Peters et al., 2009).

Instead of a cycle phase shift in preferences, Study 2 suggests a shift in women's overall attraction: Sexual attractiveness ratings were higher in the fertile phase, regardless of men's voice parameters. Similarly, a cycle phase attraction shift was recently reported for body masculinity and men's behaviors within the same dataset (Jünger et al., 2018a; 2018b). These attraction shifts might be connected to fertile phase increases in sexual motivation and desire (Arslan et al., 2018; Jones et al., 2018b; Roney & Simmons, 2013; 2016), though they were not fully supported in further exploratory analyses substituting cycle phase estimates with direct steroid hormones measurements. However, we found only partial evidence for an attraction effect in Study 1. Specifically, in Study 1, ratings were higher when progesterone levels were lower (and when E/P was higher in at least one model), which is usually the case in the fertile phase of the ovulatory cycle; hence, these results support the notion of an attraction shift. Importantly, this effect was not significant in all models. There are several possible reasons why these results differed between and within the two studies. First, different methods were used in both studies. Study 1 did use hormone levels rather than cycle phase, it used manipulated voice recordings of men reading a brief passage, and had two testing sessions per participant. Study 2, contrarily, used cycle phase and hormone levels as predictors for fertility, LH tests to validate the fertile phase, unmanipulated voice recordings of men counting, and investigated two ovulatory cycles (four testing sessions) per participant. Nevertheless, the central conclusions remain: no hormone related or cycle phase shifts in preferences were observed in either study. Second, the reported effect sizes for attraction shifts in Study 2 were small (ratings: $\gamma = 0.10$ in the main analyses). Study 1 had a smaller sample size as well as fewer test trials and therefore fewer observations than Study 2, which makes detecting this small effect more difficult. However, the differences in observations may overstate the differences in power, given that test power in both studies was high compared to previous studies. Moreover, hormone analyses in Study 1 indeed provided partial evidence for attraction shifts, observed by generally higher ratings when progesterone was lower or E/P was higher. Third, given that effect size estimates were very small, and that including random slopes might reduce test power, even the power in Study 2 might have been insufficient to detect the effect in all models. However, according to Gangestad and colleagues (2016), Study 2 should still have more than 80% power to even detect small effect sizes (with n = 112 women, within-subject design, four testing sessions each, a measurement validity of ~ .85 with using LH tests and a high correlation for ratings across phases). Fourth, although the other explanations seem to be more likely, the attraction shift effect might simply not be robust. Hence, further research should test the reliability of attraction shifts across the ovulatory cycle, investigate under which circumstances they occur and whether they correlate with a general fertile phase increase in sexual desire.

Hormonal influences

Previous studies have suggested that changes in women’s mate preferences and desire are regulated by steroid hormonal changes across the ovulatory cycle (Feinberg et al., 2006; Jones et al., 2018b; Pisanski et al., 2014; Puts, 2005; 2006; Roney & Simmons, 2013; 2016). However, our results did not reveal a clear pattern of hormonal influences on women’s attraction across the ovulatory cycle. In fact, we found different results for hormone levels across the two studies.

Progesterone predicted attractiveness ratings in Study 1 and attraction shifts in Study 2, but in different directions: negatively in Study 1 and positively in Study 2. These contradictory results remained significant in the robustness checks. The positive influence of progesterone in Study 2 is particularly counterintuitive, as progesterone levels are generally higher in the luteal phase, but we found generally higher attractiveness ratings in the fertile phase. Typically, this effect has been found in the opposite direction in previous studies and in Study 1. Critically, the negative association reported in Study 1 aligns more closely with the theoretical assumptions and findings of previous work.

Besides the puzzling effects of progesterone, E/P positively influenced attractiveness ratings in Study 1, but only in one out of three models. Regarding the overall unclear pattern of hormonal influences, we interpret these findings with caution and suggest that they need to be replicated before being interpreted further. We therefore focus here on the lack of robust, reliable hormonal influences on attraction shifts: a) The influence of progesterone and E/P remains unclear, b) estradiol did not reliably affect attractiveness ratings, and c) we found no effects of testosterone or cortisol. Therefore, we could not find evidence for hypotheses that were built on the assumptions of clear hormonal influences on cyclic shifts, e.g. the "spandrels hypothesis" that women with higher estradiol levels show stronger preferences for masculine men (Havlíček et al., 2015; Shimoda et al., 2018).

There are several possible explanations for our findings. First, we used a variety of methods across both studies (e.g. hormone analyses via LCMS vs. immunoassays) and tested participants from two populations (differing in culture and age spans) in two different labs. This might have induced important differences in the results between the two studies, and compared to previous studies. Second, perhaps hormonal influences are different for voice attraction than for other attraction to other stimuli or sexual desire, which would explain why we did not find the same hormonal influences as those predicting sexual desire (Jones et al., 2018b; Roney & Simmons, 2013; 2016). There is thus a strong need for continued research to clarify the hormonal influences on attraction shifts across the ovulatory cycle. Furthermore, it should be investigated whether hormonal influences on mate attraction vary across categories of stimuli (e.g. voices, faces, bodies). However, again, the central conclusion remain as we did not observe any hormonal influences on mate preferences for masculine voices.

No moderating effects of relationship status and perceived stress

In Study 2, we investigated whether women's relationship status or self-reported stress moderate fertile phase attraction shifts. Whereas previous studies reported that cycle shifts in women's attraction for men's bodies or behaviors were found only for partnered women, not for singles (Jünger et al., 2018a; 2018b), we did not replicate this effect for attraction to masculine voices. In line with this, Jones and colleagues (2018b) found no evidence that hormonally driven shifts in women's general sexual desire were moderated by their relationship status. However, other studies have reported that only partnered women, not singles, showed increased fertile phase sexual desire (Roney & Simmons, 2016). Thus, the effects of relationship status on psychological changes across the ovulatory cycle remain unclear. Nevertheless, our results do not support the assumptions of a dual mating strategy (that women may receive fitness benefits when forming a relationship with a reliably investing man, while seeking good genes from another man through extra-pair sexual encounters; Pillsworth & Haselton, 2006). We also did not find evidence of preference shifts for masculine voices, or a moderating effect of women's relationship status on preference shifts.

Moreover, self-reported stress did not moderate fertile phase attraction shifts. Previous studies reported different results: Stress inhibited estradiol levels (Roney & Simmons, 2015) and overrode fertile phase attraction shifts for masculine bodies (Jünger et al., 2018b) and faces (Ditzen et al., 2017), but not for men's behaviors (Jünger et al., 2018a). Hence, stress might affect only the perception of visually available cues in bodies and faces. Self-reported stress values are subjective and might not always reflect physiological stress levels (however, cortisol levels did also not influence attractiveness ratings). To investigate the impact of stress on mate attraction directly, future studies should manipulate stress experimentally. In sum, future research should investigate under which conditions and for which traits or cues cycle shifts in attraction are influenced by relationship status or self-reported stress. Additionally, other possible moderator variables should be taken into account to elucidate psychological changes across the ovulatory cycle.

Conclusion

In the current studies, we used substantially larger datasets than those in previous studies, as well as robust methods of fertility estimation and hormone assessments to investigate possible shifts in women's mate preferences and attraction to male voices across the ovulatory cycle. We found at least partial supporting evidence for ovulatory cycle shifts in attraction to men's voices, regardless of vocal masculinity, but the lack of ties to hormones is a fairly significant limitation to this finding. Attraction shifts were not moderated by women's relationship status or self-reported stress and require further research to test their robustness. We found no compelling evidence for shifts in preferences for masculine voice characteristics. Our results contrast with previous work on preference shifts for masculine voices (Feinberg et al., 2006; Pisanski et al., 2014; Puts, 2005; see also Puts, 2006), but align with recent reported null replications of cycle shifts for masculine faces, bodies and behaviors (Jones et al., 2018a; Jünger et al., 2018a; 2018b; Marcinkowska et al., 2016; 2018a; Muñoz - Reyes et al., 2014). Hence, the present research provides no compelling evidence for the good genes ovulatory shifts hypotheses and suggests that cycle shifts in preferences or attraction are more complex than previously assumed. Future research is indispensable for clarifying the conditions under which cycle shifts in women's psychology and behavior can be observed.

Acknowledgements

Study 2 was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 254142454 / GRK 2070. We thank Steven Gangestad and Alex Stern for comments on previous versions of this manuscript, and Ruben C. Arslan for valuable statistical advice.

For Study 1, we thank Marc Breedlove and Cynthia Jordan for research support, Bradly Alicea, Jill Armington, Emily Barben, Michael Burla, Kathryn Cheney, Michael DiRaimo, Melina Durhal, Rebecca Frysinger, Sana Khan, Mallory Leinenger, Heather Malinowski, Ernestine Mitchell, Joe Morehouse, Charlene Scheld, Kevin Singh, Sara Sutherland, Lisa Vroman, Tyesha Washington, and Molly Zolianbawi for assistance with study preparation and data collection, and Elizabeth Hampson and Bavani Rajakumar for assistance with hormonal assays.

For Study 2, we thank Christian Treffenstädt for assistance in the programming process, Kelly Gildersleeve for kindly providing a blueprint of an Excel sheet to calculate fertile windows and our research assistants Laura Botzet, Silvia Bradatsch, Paulina Lauer and Laura Specker-Mattißen, without whom the large data collection would not have been possible.

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Appendix D.

Curriculum vitae

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Ausbildung

seit 10/2015 **Promotionsstudentin**, DFG Graduiertenkolleg (RTG 2070) "Verstehen von Sozialbeziehungen" & Abteilung für Biologische Persönlichkeitspsychologie (Prof. Lars Penke). Abschluss voraussichtlich im August 2018.

10/2013 – 08/2015 **MSc Psychologie**, Universität Göttingen

10/2010 – 08/2013 **BSc Psychologie**, Universität Göttingen

06/2010 **Abitur** Liebigschule Gießen

Berufserfahrung und Forschungsaufenthalte

03/2018 **Forschungsaufenthalt**, University of New Mexico Albuquerque, Department of Psychology (Prof. Steven Gangestad)

09/2017 – 10/2017 **Forschungsaufenthalt**, University of California Santa Barbara, Department of Psychological and Brain Sciences (Prof. James Roney)

10/2011 – 09/2015 **Studentische Hilfskraft**, Universität Göttingen, Abteilung für Wirtschafts- und Sozialpsychologie (Prof. Stefan Schulz-Hardt)

10/2012 – 03/2013 **Tutorin**, Universität Göttingen, Abteilung für Experimentelle Psychologie (Prof. Uwe Mattler)

Publikationen (peer-reviewed)

Jünger, J., Kordsmeyer, T., Gerlach, T. M., & Penke, L. (2018). Fertile women evaluate male bodies as more attractive, regardless of masculinity. *Evolution and Human Behavior*, 39, 412-423. doi: 10.1016/j.evolhumbehav.2018.03.007

Weitere Publikationen

Buchkapitel Gerlach, T.M. & Jünger, J. (in press). Ideal partner preferences. In J. J.Ponzetti (Ed.), Encyclopedia of intimate relationships and families. Detroit: Macmillan.

Preprints Jünger, J., Motta-Mena, N. V., Cardenas, R., Bailey, D., Rosenfield, K. A., Schild, C., Penke*, L., & Puts*, D. A. (2018). Do women's preferences for masculine voices shift across the ovulatory cycle? Retrieved from psyarxiv.com/k9y7s doi: 10.17605/OSF.IO/K9Y7S

Jünger, J., Gerlach, T.M., & Penke, L. (2018). No evidence for ovulatory cycle shifts in women's preferences for men's behaviors in a pre-registered study. Retrieved from psyarxiv.com/7g3xc. doi: 10.17605/OSF.IO/7G3XC

Erfahrungen als Reviewer

Ad hoc Reviewer — British Journal of Psychology, Evolution and Human Behavior, Journal of Social and Personal Relationships, Personality and Social Psychology Bulletin

Lehrerfahrung

Lehre — **Biologische Grundlagen Interindividueller Unterschiede**. Modul für Masterstudierende (Psychologie) an der Universität Göttingen, Sommersemester 2018.

Differentielle Psychologie: Intelligenz. Seminar für Bachelorstudierende (Psychologie) an der Universität Göttingen, Sommersemester 2018.

Psychologische Diagnostik: Interview. Seminar für Bachelorstudierende (Psychologie) an der Universität Göttingen, Sommersemester 2016.

Abschlussarbeiten — **Betreuung** von 3 Bachelorarbeiten (Lara Sophie Wiechers, Vivien Vanessa Meier, Mira Hallmann) und 2 Masterarbeiten (Stephanie Rudolph, Laura-Amelie Specker-Mattißen) von Psychologiestudierenden

Professionelle Präsentationen

2017 — Jünger, J., & Schultze, T. (2017). *The Why and How of Open Science*. Vortrag im Rahmen des Workshops zu guter wissenschaftlicher Praxis für Doktoranden des Deutschen Primatenzentrums (DPZ). Göttingen, DE, 14.11.2017

Jünger, J., Meier, V.V., Kordsmeyer, T., Gerlach, T.M., & Penke, L. (2017). *Wer kommt als Sexualpartner in Frage? Die Fähigkeit Soziosexualität einzuschätzen und ihr Zusammenhang mit romantischer Anziehung*. Vortrag auf der 14. Arbeitstagung der Fachgruppe Differentielle Psychologie, Persönlichkeitspsychologie und Psychologische Diagnostik (DPPD). München, DE, 04.09. – 06.09.2017

Jünger, J., Kordsmeyer, T., & Penke, L. (2017). *Menstrual cycle shifts in female mate preferences for male body masculinity: An estrus effect instead of good genes sexual selection*? Vortrag auf der 29. Konferenz der Human Behavior and Evolution Society (HBES), Boise, ID, USA, 31.05. – 03.06.2017

2016 — Jünger, J., Arslan, R.C., Schilling, K., Gerlach, T.M., & Penke, L. (2016). *Zykluseffekte auf sexuelle Motivation und Sexualverhalten bei Frauen: Eine große, präregistrierte Studie*. Vortrag auf dem 50. Kongress der Deutschen Gesellschaft für Psychologie (DGPS), Leipzig, DE, 18.09. – 22.09.2016

Weiterbildung

2017 — **Workshop**: brms package in R – Bayesianische Mehrebenenmodelle, Paul Christian Bürkner, Göttingen, DE

Workshop: Connecting Minds in Social Neuroendocrinology and Evolution, Amanda Hahn, Boise, ID, USA

Workshop: Multilevel Structural Equation Modeling with lavaan, Yves Rosseel, Spring School on Educational Measurement, Jena, DE

Workshop: 13. Workshop für Doktoranden der Fachgruppe Differentielle Psychologie, Persönlichkeitspsychologie und psychologische Diagnostik, Manfred Schmitt, Landau, DE

Workshop: Creative Science Writing, Derek Handley, Göttingen, DE

2016 **Workshop**: R for advanced users, Holger Sennhenn-Reulen, Göttingen, DE

Workshop: Data Visualisation in R, Rick Scavetta, Göttingen, DE

Medienarbeit

29.05.2018 *Wollen Frauen Sex mit starkem oder softem Mann? Das ist dran am Hormon-Mythos*. Focus (online)

20.05.2018 *Auf der Suche nach der wahren Macht des Zyklus.* Welt am Sonntag (Zeitungsartikel)

30.04.2018 *New findings challenge the idea that women are more attracted to dominant men during the fertile phase of their ovulatory cycle*. The British Psychological society Research Digest (online)

26.01.2018 *Nope, women's cycles don't make them crave macho men*. LiveScience (online)

Mitgliedschaften

seit 2016 Göttingen Open Source and Science Initiative

Deutsche Gesellschaft für Psychologie (DGPs), Fachgruppen: Differentielle Psychologie, Persönlichkeitspsychologie und Psychologische Diagnostik (DPPD); Sozialpsychologie (FGSP)

Leibniz Science Campus "Primate Cognition" (LSC)

Weitere Fähigkeiten

Organizing Skills Organizing the Student Retreat of the Leibniz Science Campus Primate Cognition 2016

Software R, SPSS, Python, Microsoft Office

Sprachen Deutsch (Muttersprache), Englisch (fließend), Französisch (Grundkenntnisse), Russisch (Grundkenntnisse)